

The University of Chicago

THE FUNCTIONS OF THE VISUAL
AREAS OF THE CEREBRAL COR-
TEX OF THE RAT IN THE
LEARNING AND RETEN-
TION OF THE MAZE. I

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE BIO-
LOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF PSYCHOLOGY

1934

By
YÜ-CHÜAN TSANG

Private Edition, Distributed by
THE UNIVERSITY OF CHICAGO LIBRARIES
CHICAGO, ILLINOIS

Reprinted from
COMPARATIVE PSYCHOLOGY MONOGRAPHS
Vol. 10, No. 4, 1934

The University of Chicago

THE FUNCTIONS OF THE VISUAL
AREAS OF THE CEREBRAL COR-
TEX OF THE RAT IN THE
LEARNING AND RETEN-
TION OF THE MAZE. I

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE BIO-
LOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF PSYCHOLOGY
1934

By
YÜ-CHÜAN TSANG

Private Edition, Distributed by
THE UNIVERSITY OF CHICAGO LIBRARIES
CHICAGO, ILLINOIS

Reprinted from
COMPARATIVE PSYCHOLOGY MONOGRAPHS
Vol. 10, No. 4, 1934



THE FUNCTIONS OF THE VISUAL AREAS OF THE CEREBRAL CORTEX OF THE RAT IN THE LEARNING AND RETENTION OF THE MAZE. I¹

YÜ-CHÜAN TSANG

The University of Chicago

TABLE OF CONTENTS

The Problem.....	2
Method and Procedure.....	4
1. Mazes.....	4
2. Subjects.....	5
3. Training Procedure.....	6
4. Criteria of Learning.....	7
5. Surgical and Neurological Techniques.....	8
Results.....	9
1. Experimental Data.....	9
2. The Rôle of Vision in the Two Mazes.....	18
a. Inclosed Maze.....	19
b. Open Maze.....	20
3. Relative Effects of Peripheral and Cortical Blinding.....	21
a. The Character of Vision in Cortically Operated Animals.....	21
b. The Inferiority of Cortically Blinded to Peripherally Blinded Animals.....	23
(1) Inclosed Maze.....	23
(2) Open Maze.....	24
c. Probable Reasons for the Difference in Results between Inclosed and Open Mazes.....	26
4. Effects of Combined Peripheral and Cortical Blinding.....	27
a. Inclosed Maze.....	27
b. Open Maze.....	29
5. Summary of Experimental Results.....	30
6. Possible Influences of Additional Subcortical and Non-Striate Cortical Lesions on Learning Scores.....	32
a. Anatomical Topographical Relations of the Non-Striate Cortical Areas Frequently Involved in the Operations.....	32
b. Possible Influences of Subcortical Injuries.....	34
c. Possible Influences of Non-Striate Lesions Taken as a Whole....	36
d. Possible Influences of Non-Striate Lesions Taken Separately..	37

¹ The writer is deeply indebted to Professor K. S. Lashley for help and encouragement throughout this experiment and for kindly criticism in the preparation of the manuscript.

7. Some Related Findings.....	40
a. Effects of Sense Privation Versus Cortical Lesion.....	40
b. Behavior Differences between Normal, Peripherally and Corti- cally Blinded Animals.....	40
Interpretation and Discussion.....	41
Summary and Conclusions.....	48
Bibliography.....	49
Plates: Diagrams of Cerebral Lesions.....	52

THE PROBLEM

Is the function of the sensory areas of the cerebral cortex strictly sensory or imaginal, or do the areas have some additional function which is not directly related to their sensory processes but is a less specific contribution to the general efficiency of the performance? This question is by no means a new one. Prior to the emphasis on localization in cerebral physiology within the present century, the conception of dynamic functions of the cortical areas played an important part in the theories of cerebral function. Flourens ('42) spoke of an *action commune* in addition to the *action propre* of each part of the brain. In his opinion, it is on account of this fact that the nervous system forms a unitary system. Goltz ('81) also held to a similar view, considering that the capacity for attention represented the psychological aspect of the nonspecific function of the different parts of the cortex. Munk ('81) opposed this with the notion that the interaction of the specialized sensory areas by specific associative connections is sufficient to account for all the functions evident in behavior. With the emphasis on localization the cerebral cortex has come to be regarded as a mosaic of more or less specific functional areas, until recently in the light of the new findings in brain physiology the pendulum is swinging back toward the earlier and more dynamic conceptions.

In the discussion of the peripheral versus cerebral control of the maze performance by Hunter ('30, '31) and Lashley ('31b) the question mentioned above has been raised once more. Hunter does not deny other than sensory functions to the sensory areas; nevertheless, he emphasizes the sensory loss in explaining the relation between the extent of the cortical lesion and the

degree of the deficiency of maze performance. He contends that the maze habit involves a sequence of sensori-motor adjustments and that the deterioration in the capacity to learn is brought about by sensory defects, peripheral or cortical, and is in proportion to the number and extent of the sensory areas involved. On the other hand, Lashley points out that the effect of peripheral sense privation on learning is far less severe than that following the destruction of the corresponding cortical sensory projection area and that the more serious effects in the latter case are evidence for the disturbance of some general function other than cortical sensory reception. For him it is chiefly the non-sensory function of the sensory areas that counts more in the efficiency of the maze performance.

The question of the relative effects of peripheral sense privation and corresponding cortical lesion on learning is of great theoretical and methodological importance. A plausible explanation of the relative effects requires a more adequate knowledge of the functions, sensory as well as otherwise, of the sensory areas. There seems to be ample justification for a systematic investigation of the problem of specific versus general functions of the cortical sensory areas, particularly with respect to the visual system. Because it is the most specialized of all the sensory systems, a demonstration of an important non-visual function for it would be suggestive of the same situation in other less specialized sensory fields. The selection of the visual system is further justified by our fuller knowledge of its structure and function and by its easy elimination, peripheral as well as cortical.

To test the functions of the visual cortex we have adopted the following experimental procedure. (a) We first determine the character of performance in two similar functions in which vision plays different rôles. This is done by comparing the learning of two mazes of the same pattern, inclosed and open, by normal and by peripherally blinded animals. In the light of the earlier studies of Vincent ('12, '15), Miles ('27), Hunter ('29) and Lashley ('29) we have reason to believe that vision is more important for tracing the open than the inclosed maze. However, we want to test this out in a systematic manner. (b) We next determine the

influence of the removal of the visual cortex upon the learning of the two mazes. If the function of the visual cortex is exclusively sensory, the consequent retardation in learning should be proportional to the use of vision in the two mazes. In case the effect of the cortical operation exceeds that of the peripheral operation, it would evidently mean that the loss following the operation is more than visual. (c) If, as proved to be the case, the cortical destruction should produce a greater retardation of learning than the peripheral blinding, the explanation of this fact might still be one of sensory disturbance. Adult animals may have developed a system of spatial habits in visual terms which would still function in maze learning, even in the absence of vision. Damage to the visual cortex might then disturb maze learning by disrupting the visual space-habits. The alternative to this would be some non-visual function of the visual cortex. To test these alternatives animals are blinded in infancy before the eyes open naturally, thus eliminating the opportunity for building any visual space-habit; and later the effects of injuries to the visual areas are studied.

In the present report we shall confine ourselves to the results reached in the first two steps mentioned above. The results of the third step will form the subject matter of a separate paper.

METHOD AND PROCEDURE

1. *Mazes*

The inclosed maze is a modification of Lashley's maze III ('29). It measures 147 cm. long and 99 cm. wide, divided into fifteen sections, eight being culs-de-sac. The dotted line in the accompanying figure indicates the correct pathway to the food box. The runway is 6 cm. wide with side-walls 9 cm. high. The starting and food boxes occupy such positions that they do not change the general plan of the maze. Their dimensions are the same as those of a shorter maze section. Both boxes are provided with swing doors controlled by threads. The whole maze is painted dead black. It is raised 51 cm. from the floor and covered with

wire mesh. Separate covers of the same material are hinged to starting and food boxes.

The open maze is of approximately the same dimensions as the inclosed, but with no side-walls. The starting and feeding parts of this maze assume the form of a platform. The maze is surrounded by a rectangular screen of black cloth to shut off partially the irrelevant visual distractions.

The visual sensibility of most of the cortically blinded animals was tested on the Lashley jumping apparatus of which several

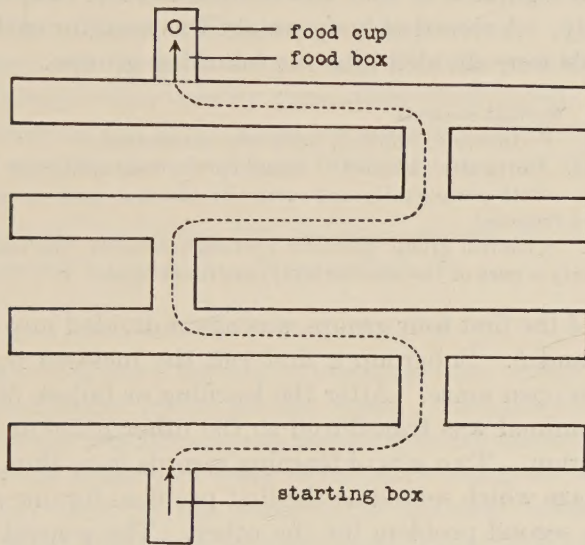


FIG. 1. GROUND PLAN OF THE INCLOSED MAZE

models have been in use in the Chicago laboratory. No description of this apparatus is necessary. The reader is referred to the original literature (Lashley, '30).

2. Subjects

Ninety-six female rats from the laboratory colony were used in this study. They were hybrids of several strains of *Mus norvegicus* with the hooded blood predominating. Among the animals used Numbers 1 to 36 were albinos extracted from the hooded

stock; all the others were hooded. The distribution of these two kinds of rats in the groups was approximately the same. The age ranged from 100 to 150 days at the start of training. Their vision was normal at the beginning of the experiment. The records of several animals were dropped out of account because of ill health, death or infection of the brain.

3. Training Procedure

Hunger was used as incentive to learning. The duration of feeding was regulated so that the animals did not take on weight too abruptly. A record of body weight was kept for each animal. The animals were divided into the following groups:

Group I. Normal controls.

Group II. Peripherally blinded: both eyes enucleated.

Group III. Cortically "blinded": visual cortex destroyed, eyes intact.

Group IV. Both peripherally and cortically blinded: both eyes and visual cortex removed.

Group V. A control group, partially cortically blinded: the lesion involving only a part of the area striata, eyes functional.

Each one of the first four groups was again divided into two subgroups, *a* and *b*. Subgroup *a* first ran the inclosed maze, subgroup *b* the open maze. After the learning or failure of the first maze, the animal was transferred to the other maze and trained to the criterion. Two sets of learning records were thus obtained for each maze which served as the first problem for one subgroup and as the second problem for the other. The general effect of blinding on each maze performance was deduced by averaging the scores of the subgroups *a* and *b* for the same problem as a partial control of the transfer effects. Group V was trained in the inclosed maze only.

The regular training took place in the afternoon. The laboratory was artificially and uniformly lighted. Prior to the start of the training in the maze, whether it be the first or the second problem, the animal was fed in the food box or on the platform five minutes daily for three days in succession to get it partially accustomed to the maze situation and to handling, and to associate the maze with food. With the first problem the animal was given a

single trial on the first day, two trials on the second day and five trials per day thereafter until the criterion of mastery, ten consecutive errorless trials, was reached or until 150 trials had been given, at which the training was discontinued. For the second problem two trials were given on the first day and five trials per day thereafter. After each successful trial the animal was rewarded with a few bites and then transferred to the starting box or platform for the next run. At the close of the daily training the animal was given its ration in the home cage.

Every effort was made to keep the experimental conditions constant throughout. Olfactory, somesthetic and other sensory factors were not specially controlled. For our problem it makes little difference what sensory cues, other than visual, the animal uses in learning the maze, since we are primarily comparing the effect of peripheral and cortical blinding upon the formation of the habit.

The general procedure for training animals on the jumping apparatus will be given in a later section.

4. Criteria of Learning

The three ordinary criteria of learning, time, errors and trials, have been adopted in the present study. Records were kept for each rat of the total time spent and total errors made in each trial and the total number of trials required to attain the standard of proficiency, that is, ten consecutive errorless trials. On the completion of 150 trials, as mentioned before, training was discontinued and the total number of errorless runs made in the 150 trials was computed. Two types of errors were recorded: (a) entrance into blind runways as the animal was moving forward in the direction of the food box or platform; (b) retracing over the sections of the true path or into the blind runways while the animal was going toward the starting box or platform.

Of the three criteria the error score is the most reliable. But it should be added that the reliability of the different criteria varies somewhat with the purpose of the study. The gross time score is the most unreliable, because, as Tolman ('21) has pointed out, it is made up of two variables not necessarily related: the "pure

speedness," being perhaps a matter of physiological tempo or of temperamental or emotional endowment, and the error-eliminating ability. This is particularly true with the operated animals; here time may mean inactivity. The trial score cannot be evaluated in terms of internal consistency. It may be considerably increased by a few errors and is further distorted in the present study by the arbitrary limit of 150 trials set to the animals. However, it should be noted that our criterion of ten consecutive errorless trials is much higher than ordinarily adopted and the reliability of the trial score is thereby increased considerably. The error score is immune from those sources of error mentioned above and presents the highest consistency. Accordingly, in interpreting our results we shall lay special emphasis on the error scores. The time and trial scores are also presented and give essentially the same results.

5. Surgical and Neurological Techniques

All operations were done under deep ether anesthesia with antiseptic technique. The rats in Group II were blinded peripherally by enucleation of the eyes. This could be done rapidly with little or no hemorrhage. Groups III and IV were cortically "blinded" by destruction of the visual cortex. The visual cortex was removed by an electric thermo-cautery through a small trephine hole on the skull in front of the parieto-occipital suture. The eyes of Group IV were enucleated at the same operation. An attempt was made to destroy the visual cortex in its entirety, projection as well as "association" parts. Figure 2 is a reproduction of Fortuyn's ('14) cyto-architectural areas of the rat's cerebrum as modified by Lashley ('29). The strictly visual field, area striata, is largely within the boundary of area w (Herrick, '26, Volkmann, '26, Rose, '29, Lashley, '31). With Group V the lesion was intended for the area striata only. For the operation we used a small scalpel instead of the thermo-cautery.

The cortically operated animals were allowed ten days for recovery. At the end of this period training was begun. The allowance for the peripherally blinded animals was three days.

At the completion of training the animal was brought to necropsy. The brain was removed, fixed, cut and stained with

iron-hematoxylin. A reconstruction of the cerebral lesion was made on a conventional diagram of rat's cerebrum following Lashley's procedure ('29). For Group V we employed the thionin technique, the sections being much thinner for the convenience of histological examination of the chromatolysis of cells in the lateral geniculate bodies. Rough, off-hand reconstructions were made of the degenerated parts of the last mentioned nuclei as a check on the extent of lesion in the area striata. The total area of cerebral lesion in each case was measured from the diagram with a

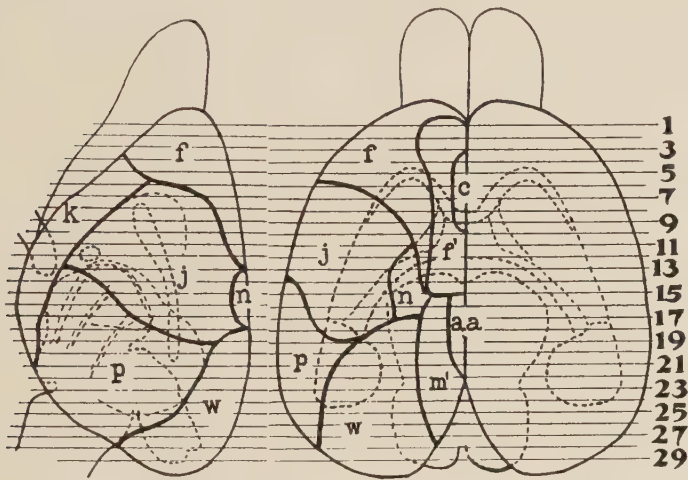


FIG. 2. FORTUYN'S CYTO-ARCHITECTURAL AREAS OF THE RAT'S CEREBRUM AS MODIFIED BY LASHLEY

planimeter and expressed as the percentage of the total surface area of the cerebrum. The area of the non-striate field most involved in addition to the destruction of area striata was also similarly measured and expressed.

The reconstructions of the brain lesions of animals in the various groups are shown in the plates at the end of this report.

RESULTS

1. *Experimental Data*

In Table I are given the individual records of learning of the inclosed and open mazes by the normal animals. Subgroup Ia

was first trained in the inclosed and then transferred to the open maze; while Subgroup Ib was first trained in the open and then in the inclosed maze. Total time spent, total errors made and total

TABLE I
Individual Records of Learning of the Inclosed and the Open Mazes Made by the Normal Controls

Subgroup Ia ran first the inclosed and then the open maze; Subgroup Ib ran first the open and then the inclosed maze. Total time, total errors and total trials preceding the ten consecutive errorless trials are given for each animal.

ANIMAL GROUP	NUMBER	INCLOSED MAZE			OPEN MAZE		
		Time	Errors	Trials	Time	Errors	Trials
		<i>seconds</i>			<i>seconds</i>		
Ia	9	1,988	224	26	383	22	16
	24	3,769	158	97	3,323	163	75
	25	2,033	35	18	313	14	12
	27	3,135	102	32	3,076	83	92
	37	923	56	37	1,485	71	34
	38	276	27	11	272	17	5
	41	8,512	233	61	1,291	57	11
	43	415	28	11	1,236	68	22
	45	2,373	73	31	366	19	16
	46	1,347	92	50	463	26	21
	63	947	59	46	199	17	12
Ib	8	1,521	156	41	472	18	58
	11	354	23	22	2,616	87	47
	26	994	77	46	3,453	101	48
	29	662	37	31	4,083	64	49
	39	1,032	60	68	1,980	99	22
	42	177	10	10	369	15	17
	44	708	43	60	2,375	89	27
	47	2,946	87	24	1,989	52	2
	48	1,014	112	26	525	48	23
	81	377	25	19	5,034	186	58
	94	638	41	69	1,241	65	29

trials taken preceding the ten consecutive errorless trials are given for each case.

In Table II we present the individual learning scores of the peripherally blinded animals for the inclosed and the open mazes. Subgroup IIa ran first the inclosed and then the open maze; Sub-

group IIb ran first the open and then the inclosed maze. Total time, total errors and total trials preceding the ten consecutive errorless trials, or within 150 trials in case of failure, are given.

TABLE II

Individual Records of Learning of the Inclosed and the Open Mazes Made by the Peripherally Blinded Animals

Subgroup IIa ran first the inclosed and then the open maze; Subgroup IIb ran first the open and then the inclosed maze. Total time, total errors and total trials preceding the ten consecutive errorless trials, or on the completion of the arbitrary number of one hundred and fifty trials at which training was discontinued, are given for each animal.

ANIMAL GROUP	NUMBER	INCLOSED MAZE			OPEN MAZE		
		Time	Errors	Trials	Time	Errors	Trials
		<i>seconds</i>			<i>seconds</i>		
IIa	30	639	54	13	1,902	99	72
	33	8,148	501	101	17,623	651	150 (49)*
	34	296	14	6	1,565	52	56
	35	710	45	23	1,674	98	22
	36	558	53	43	795	60	64
	51	525	28	9	634	33	39
	52	493	35	10	1,028	36	15
	53	836	37	26	7,302	287	150 (60)
	54	4,404	320	86	18,823	614	150 (36)
	61	1,748	62	51	1,379	88	55
	78	2,440	176	93	2,149	148	126
IIb	28	2,356	114	41	25,123	903	150 (26)
	31	542	18	13	2,076	68	62
	32	534	30	17	889	31	28
	40	2,552	181	102	10,747	483	150 (31)
	55	211	16	7	2,190	68	63
	56	141	12	5	572	31	23
	57	4,461	391	132	3,471	441	89
	58	437	26	17	820	46	19
	70	2,171	90	75	7,936	299	150 (56)
	71	652	41	44	11,229	476	150 (46)
	76	1,082	50	34	7,510	241	150 (57)

* Figures in parentheses are errorless trials.

The individual learning scores of the cortically blinded animals for the two mazes are summarized in Table III. The percentage of the total neopallium removed in each case is given. Subgroup

TABLE III

Individual Records of Learning of the Inclosed and the Open Mazes Made by the Cortically Blinded Animals

The percentage of the total neopallium destroyed is given at the left. Brain diagrams illustrating the lesions are given under corresponding numbers in the plates at the end of this report. Subgroup IIIa ran first the inclosed and then the open maze; Subgroup IIIb ran first the open and then the inclosed maze. Group V was trained in the inclosed maze only. Total time, total errors and total trials preceding the ten consecutive errorless trials, or on the completion of the arbitrary number of one hundred and fifty trials at which training was discontinued, are given for each animal.

ANIMAL GROUP	NUMBER	PERCENT-AGE OF LESION	INCLOSED MAZE			OPEN MAZE		
			Time	Errors	Trials	Time	Errors	Trials
			<i>seconds</i>			<i>seconds</i>		
IIIa	2	21.1	2,387	597	150 (5)	2,798	490	150 (33)
	6	22.1	7,185	885	150 (15)	2,194	267	127
	18	30.4	2,566	379	95	1,702	260	75
	59	14.9	8,430	978	150 (30)	7,791	1,037	107
	62*	22.3	2,054	281	112	713	136	30
	73*	18.3	3,261	472	150 (46)	2,167	256	40
	75*	24.0	3,710	604	150 (17)	1,585	296	119
	77*	32.5	2,605	671	150 (0)	790	106	51
	80*	34.9	3,028	636	150 (25)	2,252	353	115
	82*	27.7	1,931	310	96	947	150	37
IIIb	7	28.5	1,154	93	31	7,641	489	150 (38)
	14	31.5	1,986	374	130	4,073	810	150 (18)
	15	18.7	4,274	769	150 (0)	8,674	1,780	137
	16*	19.2	3,642	535	132	5,029	722	150 (20)
	17	20.0	413	40	14	2,213	247	110
	21*	32.6	1,882	362	63	2,788	501	150 (48)
	68*	14.3	2,231	177	83	2,684	250	138
	79*	31.1	890	201	53	1,281	144	71
	83*	24.0	1,985	166	81	954	166	73
	84*	31.1	890	181	27	1,474	248	85
	87*	31.1	1,029	296	58	852	211	53
V	5	6.0	15,982	386	150 (72)			
	10	6.2	3,610	266	79			
	60	7.2	5,228	677	150 (36)			
	72	6.6	1,559	91	45			
	88	6.2	3,435	270	60			
	97	8.7	30,927	524	150 (63)			
	98	5.7	2,483	380	150 (64)			
	101	7.9	12,705	452	150 (59)			
	102	7.5	3,552	137	150 (86)			
	106	11.3	18,698	595	150 (53)			
	108	7.1	778	49	52			
	109	7.1	3,042	221	150 (74)			
	110	9.2	1,007	81	68			

* Animals whose visual sensitivity has been tested on the jumping apparatus.

IIIa was first trained in the inclosed and then in the open maze; with Subgroup IIIb the order was reversed. Time, error and trial scores are similarly presented for each case. The individual

TABLE IV

Individual Records of Learning of the Inclosed and the Open Mazes Made by Animals Both Peripherally and Cortically Blinded

The percentage of the total neopallium destroyed is given at the left. Brain diagrams illustrating the lesions are given under corresponding numbers in the plates at the end of this report. Subgroup IVa ran first the inclosed and then the open maze; Subgroup IVb ran first the open and then the inclosed maze. Total time, total errors and total trials preceding the ten consecutive errorless trials, or on the completion of the arbitrary number of one hundred and fifty trials at which training was discontinued, are given for each animal.

ANIMAL GROUP	NUMBER	PERCENT-AGE OF LESION	INCLOSED MAZE			OPEN MAZE		
			Time	Errors	Trials	Time	Errors	Trials
			<i>seconds</i>			<i>seconds</i>		
IVa	1	19.1	1,956	261	93	6,637	761	150 (14)
	3	27.9	13,339	2,725	150 (0)	9,313	1,515	150 (6)
	20	35.1	5,036	524	119	2,356	316	150 (45)
	22	35.3	7,792	1,107	107	8,942	843	150 (5)
	23	33.9	3,326	755	150 (10)	8,028	1,142	150 (2)
	50	28.5	1,913	350	128	3,667	600	150 (18)
	64	28.5	2,585	446	150 (52)	2,516	301	121
	85	32.5	2,781	630	131	2,121	407	150 (24)
IVb	90	34.0	11,551	2,343	150 (0)	12,951	1,517	150 (0)
	4	30.2	28,916	1,931	150 (3)	10,878	2,117	150 (0)
	12	33.4	2,288	392	117	4,879	1,122	150 (1)
	13	27.2	1,766	178	107	6,783	897	150 (13)
	65	31.3	1,681	332	117	5,061	886	150 (28)
	66	30.2	3,121	595	116	11,829	1,645	150 (24)
	67	29.2	2,041	274	48	3,756	716	150 (30)
	69	35.8	2,547	419	87	3,309	702	150 (11)
	(74)*	(25.3)	(32,468)	(3,580)	(150) (0)	(17,006)	(1,911)	(150) (0)
	89	21.5	542	54	17	3,807	343	150 (69)

* The unusually poor scores of this animal have been dropped out from group averages.

scores and percentages of lesion of Group V, the partially cortically blinded, are also appended to the same table.

The individual records of the both peripherally and cortically

TABLE V

Comparison of the Group Average Scores of Normal Controls and of Animals Blinded Peripherally, Cortically and in Both Ways for the Inclosed Maze When This Was Either Their First or Second Problem

The averages are based upon all cases in each group (except Number 74 in IVb) which reached the criterion of learning or completed the arbitrary number of one hundred and fifty trials. The average percentage of cerebral lesions is given for each cortically operated subgroup. Averages of time, errors and trials are given together with their respective probable errors. Under "Difference" the absolute difference between the normal and the operated subgroups is given; under "Percentage" the absolute difference is expressed as percentage of the corresponding average of the normal subgroup; and under "Average Retardation" the average of the three percentage differences is presented.

ANIMAL GROUP	NUMBER OF CASES	AVERAGE PERCENT- AGE OF LESIONS	CRITERIA	AVERAGE SCORES		DIFFERENCE	PERCENTAGE	AVERAGE RETARDA- TION
Maze as First Problem								
Ia, Normal	11		Time Errors Trials	2,338.00 ± 449.67 98.82 ± 14.44 38.18 ± 4.86				
IIa, Peripherally Blinded	11		Time Errors Trials	1,891.00 ± 466.46 120.45 ± 30.01 41.91 ± 6.98	-447.00 21.63 3.73	-19.12 21.89 9.77		4.18
IIIa, Cortically Blinded	10	24.8	Time Errors Trials	3,716.00 ± 453.72 581.30 ± 46.67 135.30 ± 4.88	1,378.00 482.48 97.12	58.94 488.24 254.37		267.18
IVa, Peripherally and Cortically Blinded	9	30.5	Time Errors Trials	5,587.00 ± 916.24 1,015.67 ± 190.89 130.89 ± 4.51	3,249.00 916.85 92.71	138.96 927.80 242.82		436.53
V, Partially Corti- cally Blinded	13	7.44	Time Errors Trials	7,924.00 ± 1,635.37 317.62 ± 36.70 115.69 ± 8.23	5,586.00 218.80 77.51	238.92 221.41 203.01		221.11
Maze as Second Problem								
Ib, Normal	11		Time Errors Trials	948.00 ± 147.95 61.00 ± 8.49 37.82 ± 3.97				

TABLE V—*Concluded*

ANIMAL GROUP	NUMBER OF CASES	AVERAGE PERCENT- AGE OF LESIONS	CRITERIA	AVERAGE SCORES	DIFFERENCE	PERCENTAGE	AVERAGE RETARDA- TION
Maze as Second Problem— <i>Concluded</i>							
IIb, Peripherally Blinded	11		Time	1,376.00 $\pm$ 261.90	428.00	45.15	35.54
			Errors	88.09 $\pm$ 21.90	27.09	44.41	
			Trials	44.27 $\pm$ 8.10	6.45	17.05	
IIIb, Cortically Blinded	11	25.7	Time	1,852.00 $\pm$ 232.05	904.00	95.36	189.65
			Errors	290.36 $\pm$ 41.14	229.36	376.00	
			Trials	74.73 $\pm$ 8.85	36.91	97.59	
IVb, Peripherally and Cortically Blinded	8	29.9	Time	5,363.00 $\pm$ 2,128.28	4,415.00	465.72	457.38
			Errors	521.88 $\pm$ 131.98	460.88	755.54	
			Trials	94.88 $\pm$ 9.58	57.06	150.87	

blinded animals for the two mazes are shown in Table IV. The percentage of the total cortex destroyed is given for each case. Subgroup IVa ran first the inclosed, and then the open maze; the order was reversed with Subgroup IVb. Time, error and trial scores of each animal are similarly presented.

The average scores, time spent, errors and trials made, have been computed for all normal and operated groups for each maze. The records of animals which failed to learn the problem with 150 trials were averaged together with the successful cases of the same group. The group average scores with their probable errors are given in Tables V and VI. Group scores of the four subgroups Ia, IIa, IIIa, and IVa for the inclosed maze, which was run as their first problem, are shown in Table V. The absolute differences in the scores between the normal subgroup and the differently blinded subgroups are presented. The differences are also expressed as the percentages of the corresponding normal scores. The average of the three percentage differences has been computed for each operated subgroup and designated as the average retardation of that subgroup, as compared with the normal

TABLE VI

Comparison of the Group Average Scores of Normal Controls and of Animals Blinded Peripherally, Cortically and in Both Ways for the Open Maze When This Was Either Their First or Second Problem

The averages are based upon all cases in each group (except Number 74 in IVb) which reached the criterion of learning or completed the arbitrary number of one hundred and fifty trials. The average percentage of cerebral lesions is given for each cortically operated subgroup. Averages of time, errors, and trials are given together with their respective probable errors. Under "Difference" the absolute difference between the normal and the operated subgroups is given; under "Percentage" the absolute difference is expressed as percentage of the corresponding average of the normal subgroup; and under "Average Retardation" the average of the three percentage differences is presented.

ANIMAL GROUP	NUMBER OF CASES	AVERAGE PERCENTAGE OF LESIONS	CRITERIA	AVERAGE SCORES	DIFFERENCE	PERCENTAGE	AVERAGE RETARDATION
Maze as First Problem							
Ib, Normal	11		Time Errors Trials	2,194.00 ± 297.08 74.91 ± 9.14 34.55 ± 3.57			
IIb, Peripherally Blinded	11		Time Errors Trials	6,597.00 ± 1,418.64 280.64 ± 53.55 94.00 ± 11.08	4,403.00 205.73 59.45	200.68 274.64 172.07	215.80
IIIb, Cortically Blinded	11	25.7	Time Errors Trials	3,424.00 ± 519.29 506.18 ± 92.80 115.18 ± 7.35	1,230.00 431.27 80.63	56.06 575.72 233.37	288.39
IVb, Peripherally and Cortically Blinded	8	29.9	Time Errors Trials	6,288.00 ± 739.05 1,053.50 ± 127.25 150.00 ± 0.00	4,094.00 978.59 115.45	186.60 1,306.35 334.15	609.03
Maze as Second Problem							
Ia, Normal	11		Time Errors Trials	1,128.00 ± 217.56 50.64 ± 8.76 28.73 ± 5.49			
IIa, Peripherally Blinded	11		Time Errors Trials	4,989.00 ± 1,316.48 196.91 ± 43.93 81.73 ± 10.17	3,861.00 146.27 53.00	342.29 288.84 184.48	271.87

TABLE VI—*Concluded*

ANIMAL GROUP	NUMBER OF CASES	AVERAGE PERCENT- AGE OF LESIONS	CRITERIA	AVERAGE SCORES		DIFFERENCE	PERCENTAGE	AVERAGE RETARDA- TION
Maze as Second Problem— <i>Concluded</i>								
IIIa, Cortically Blinded	10	24.8	Time	2,294.00 ±	415.67	1,166.00	103.37	287.10
			Errors	335.10 ±	54.90	284.46	561.73	
			Trials	85.10 ±	8.84	56.37	196.21	
IVa, Peripherally and Cortically Blinded	9	30.5	Time	6,281.00 ±	813.02	5,153.00	456.83	797.27
			Errors	822.44 ±	101.07	771.80	1,524.09	
			Trials	146.78 ±	2.04	118.05	410.89	

scores for the same maze. The average percentages of lesions for the cortically operated subgroups are also appended to the same table.

We have obtained another set of learning records for the inclosed maze with Subgroups Ib, IIb, IIIb and IVb after the completion of their learning of the open maze or after the failure in it with 150 trials. The average percentages of lesions for the cortically operated subgroups are given. Their average records together with the corresponding probable errors, the absolute differences, the percentage differences in the three criteria of learning and the average retardations of the operated subgroups are summarized in Table V.

Similarly, the group average records of the four subgroups Ib, IIb, IIIb and IVb for the open maze, which was their first problem, are presented in Table VI, where the absolute differences, percentage differences and average retardations of the differently blinded subgroups are to be found. The average records of the four subgroups Ia, IIa, IIIa and IVa which ran the open maze as the second problem and the corresponding absolute differences, percentage differences and average retardations of the operated subgroups are also referred to the same table.

The data of those cortically blinded animals which had been

tested on the jumping apparatus will be briefly stated in a later section.

2. *The Rôle of Vision in the Two Mazes*

Our results show definitely that the open maze is much easier than the inclosed for the normals as judged by all the three criteria of learning. In the average scores the normal Subgroup Ib, first trained in the open maze (see Table VI), is superior to the normal Subgroup Ia, first trained in the inclosed maze (Table V). With the interchange of mazes this relation is reversed: the same Subgroup Ib when tested in the inclosed maze (Table V) is inferior to Subgroup Ia as tested in the open maze (Table VI). As a concrete illustration we reproduce below their error records for the two mazes:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
Ia (Normal)	Inclosed maze, first	98.82 ± 14.44	23.91 ± 17.07
Ib (Normal)	Open maze, first	74.91 ± 9.14	
Ib (Normal)	Inclosed maze, second	61.00 ± 8.49	10.36 ± 12.20
Ia (Normal)	Open maze, second	50.64 ± 8.76	

We thus see that normal animals invariably made a lower error score in the open than in the inclosed maze, no matter whether the open maze was run as the first or the second problem.

For the peripherally blinded animals the open maze is unquestionably more difficult. This statement is amply justified by the differences between the average records of the peripherally blinded Subgroup IIb in the open maze (Table VI) and the similarly operated Subgroup IIa in the inclosed maze (Table V), and by the complete reversal of the former relations in the records for their second problem (Tables V and VI). We again present their error scores for the mazes in a tabular form at top of page 19. It is plain that the peripherally blinded rats had much greater difficulty in tracing the open maze. They made more than twice as many errors in the open maze as the similarly operated animals in the inclosed.

The relative difficulty of the mazes varies with the presence or

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIa (Peripherally blinded)	Inclosed maze, first	120.45 ± 30.01	160.19 ± 61.39
IIb (Peripherally blinded)	Open maze, first	280.64 ± 53.55	
IIb (Peripherally blinded)	Inclosed maze, second	88.09 ± 21.90	108.82 ± 49.09
IIa (Peripherally blinded)	Open maze, second	196.91 ± 43.93	

absence of vision. This suggests the important rôle which vision plays in the open maze. We now compare the learning scores of the normal and peripherally blinded for the same maze. We shall treat the maze problems separately.

a. Inclosed Maze. It is clear from Table V that the peripherally blinded rats, Subgroups IIa and IIb, which ran the inclosed maze as the first and second problem respectively were close matches of the normals. The absolute differences in time, error and trial scores are not much greater than the chance deviations of the normal scores. Let us compare their error scores.

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
Ia (Normal)	Inclosed maze, first	98.82 ± 14.44	21.63 ± 33.30
IIa (Peripherally blinded)	Inclosed maze, first	120.45 ± 30.01	
Ib (Normal)	Inclosed maze, second	61.00 ± 8.49	27.09 ± 23.49
IIb (Peripherally blinded)	Inclosed maze, second	88.09 ± 21.90	

The average retardations of these animals are slight when compared with effects of cortical blinding to be presented later, 4.18 per cent for Subgroup IIa and 35.54 per cent for Subgroup IIb. By averaging these two we have arrived at a combined retardation of 19.86 per cent. This probably represents a real difference, but in no case is the difference in maze efficiency between the normals and the peripherally blinded statistically reliable. Furthermore, there is not a single failure among the peripherally blinded in

the inclosed maze with 150 trials (Table VII). The effect of peripheral privation of vision on the learning of the inclosed maze is thus not great and of questionable reliability.

b. Open Maze. An entirely different situation exists in the open maze. The peripherally blinded animals are far inferior to the normal controls in maze efficiency (Table VI). We take up particularly the error scores for the open maze of the peripherally blinded Subgroups IIb and IIa which ran this maze as the first and second problem respectively, together with the normal error scores for a comparison:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
Ib (Normal)	Open maze, first	74.91 $\pm$ 9.14	205.73 $\pm$ 54.32
IIb (Peripherally blinded)	Open maze, first	280.64 $\pm$ 53.55	
Ia (Normal)	Open maze, second	50.64 $\pm$ 8.76	146.27 $\pm$ 44.79
IIa (Peripherally blinded)	Open maze, second	196.91 $\pm$ 43.93	

The peripherally blinded animals made about four times as many errors as the normals. Subgroups IIb and IIa show retardations of 215.80 per cent and 271.87 per cent respectively, with a combined retardation of 243.83 per cent. The performance of the animals without eyes in the open maze is more than twice as poor as that of animals with normal eyes. Otherwise expressed, the retardation of the peripherally blinded in the open maze is more than twelve times that of the same kind of animals in the inclosed maze of exactly the same pattern. In contrast to the straight success of the normals, five out of eleven rats in Subgroup IIb or 45.45 per cent and three out of eleven rats in Subgroup IIa or 27.27 per cent failed the open problem, the combined percentage of failures being 36.36 per cent (Table VII).

In short, for the inclosed maze, the effects of the removal of the eyes upon learning are slight and statistically insignificant; whereas for the open maze peripheral blinding has tremendous effects upon the learning scores. The greater rôle of vision in tracing the open maze, as alluded to by previous workers, is thus

established beyond any doubt. Thus, in the two similar functions vision plays very different rôles, as expected at the formulation of our research problem. We are now in a position to test the function of the visual cortex in learning the two mazes. If it is purely sensory in function, as said before, cortical blinding should produce the same degree of retardation in the two mazes as does peripheral blinding.

TABLE VII

Number and Percentage of Failures in the Animal Groups for Each Maze

Subgroups a's ran first the inclosed maze; Subgroups b's, the open maze. Group V ran the inclosed maze only.

ANIMAL GROUP	NUMBER OF CASES	INCLOSED MAZE		OPEN MAZE	
		Number of Failures	Percentage of Failures	Number of Failures	Percentage of Failures
Ia, Normal	11	0	0.00	0	0.00
IIa, Peripherally Blinded	11	0	0.00	3	27.27
IIIa, Cortically Blinded	10	7	70.00	1	10.00
IVa, Peripherally and Cortically Blinded	9	4	44.44	8	88.88
Ib, Normal	11	0	0.00	0	0.0
IIb, Peripherally Blinded	11	0	0.00	5	45.45
IIIb, Cortically Blinded	11	1	9.09	4	36.36
IVb, Peripherally and Cortically Blinded	8	1	12.50	8	100.00
V, Partially Cortically Blinded	13	8	61.54		

3. Relative Effects of Peripheral and Cortical Blinding

a. The Character of Vision in Cortically Operated Animals.

Before presenting the effects of cortical blinding on maze efficiency we shall state very briefly the condition of visual sensitivity of the cortically operated animals. In the light of the researches of Lashley and his associates we feel sure that animals thus operated still preserve some visual sensitivity. However, we have tested this matter ourselves.

We have trained on the Lashley jumping apparatus six rats of Subgroup IIIa which ran first the inclosed maze and seven rats in Subgroup IIIb which ran first the open maze (cases starred in

Table III). Other animals in these subgroups had already been brought to necropsy when we decided to add this item in our experiment. The animals were trained to jump from a starting platform to a feeding platform against and through one of two cardboard doors on which were glued the stimulus patches. When the animal jumped at the positive stimulus the door was knocked aside and he was rewarded by some bites of food; when the negative stimulus was jumped at he would fall down and get no food. The jumping apparatus was placed against the white wall of the laboratory. The rats learned first to walk, then to jump, through an open door to reach food. After that we put on the white and black cardboards. Ten trials were given daily to each animal. Without any special training, all the animals tested, except two (Numbers 21 and 79 of Subgroup IIIb), jumped directly against the white stimulus card and made twenty errorless jumps consecutively, which was our criterion of mastery for the black-white discrimination.

All these successful animals in the brightness vision test were next subject to the test of horizontal versus vertical stripes. Stripes of glossy white paper, 2 cm. wide, were glued to black cardboard leaving intervals of the same width between them. The horizontal stripes were the positive stimulus. None of the animals passed this test in one hundred trials, at the end of which training was discontinued. The average of errorless trials of the six animals of Subgroup IIIa is 49.50; and that for the seven animals of Subgroup IIIb is 48.57, both being well within the limits of sheer chance. The absence of pattern vision in these animals has thus been proved.

Lashley ('29) suggests the use of pattern vision in the open maze habit. With normal animals the open maze permits more free use of vision for general orientation and for discrimination of the immediate maze pattern. This is chiefly responsible for the more rapid learning of the open maze. Moreover, we found that the cortically blinded animals made fewer errors in the open than in the inclosed maze, when these were their first problems (Tables V and VI). The error score of Subgroup IIIb for the open maze is 506.18, and that of Subgroup IIIa for the inclosed maze is

581.30. Since their visual sensitivity was limited to brightness and position, the natural suggestion is that in the absence of pattern vision this residual visual sensitivity was probably still able to supply visual cues for the general orientation and consequently for the better performance in the open maze.

This relation in the error scores of the same subgroups for the two mazes is reversed when they were run as the second problems. The error score of Subgroup IIIa for the open maze is 335.10 and that of Subgroup IIIb for the inclosed is 290.36. This immediately casts doubt upon the superiority of the open maze subgroup. This problem needs more thorough investigation. Our results do not show decisively just how far pattern vision is or is not essential for the open maze habit. What seems to be true is simply that in the absence of pattern vision the residual position and brightness vision is still capable of providing directive cues for tracing the open maze.

Another fact suggesting the greater use of the residual vision in the open maze comes from the behavior side. Animals with normal and even such partial vision were more or less "seeing" their way to the food platform in the open maze. Their final running seemed to be less automatic than that of similar animals in the inclosed maze, although we are not in a position to furnish quantitative data on the last point.

b. The Inferiority of Cortically Blinded to Peripherally Blinded Animals. (1) Inclosed Maze. Table V presents the average learning records for the inclosed maze of the cortically blinded animals and those of the peripherally blinded for the same problem. The striking inferiority of the former to the latter is convincingly exemplified by the error scores of the cortically blinded Subgroup IIIa which first ran the inclosed maze, and of the peripherally blinded Subgroup IIa for the same maze:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIa (Peripherally blinded)	Inclosed maze, first	120.45 $\pm$ 30.01	460.85 $\pm$ 55.49
IIIa (Cortically blinded)	Inclosed maze, first	581.30 $\pm$ 46.67	

The cortically blinded made nearly five times as many errors as the peripherally blinded. Time and trial scores also show similar disproportionate retardations. The average retardation of Subgroup IIIa amounts to 267.18 per cent, being sixty-six times the retardation of Subgroup IIa, 4.18 per cent. Seven out of ten animals or 70 per cent failed to reach the criterion of mastery within the time limit, in contrast to the straight success of the peripherally blinded.

We find the same situation in the records of the cortically blinded Subgroup IIIb which ran the inclosed maze as the second problem (Table V). They were much more retarded than the peripherally blinded Subgroup IIb in the same maze. Let us compare their error scores:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIb (Peripherally blinded)	Inclosed maze, second	88.09 $\pm$ 21.90	202.27 $\pm$ 46.61
IIIb (Cortically blinded)	Inclosed maze, second	290.36 $\pm$ 41.14	

The cortically blinded made more than three times as many errors as the peripherally blinded. The same tendency is obvious in the time and trial scores. The average retardation of the cortically blinded Subgroup IIIb is 189.65 per cent, being five times that of the peripherally blinded Subgroup IIb, which is 35.54 per cent. One failure was recorded in the eleven cases of Subgroup IIIb, or 9.09 per cent, whereas there was none in Subgroup IIb.

The combined retardation of the two cortically blinded Subgroups IIIa and IIIb for the inclosed maze is 228.41 per cent, being eleven times that of the peripherally blinded Subgroups IIa and IIb, 19.86 per cent. Their combined percentage of failures is 39.54 in sharp contrast to the clean record of success of the peripherally blinded.

(2) *Open Maze.* What has been said of the inclosed maze is generally true of the open maze, though to a lesser degree. Let us select from Table VI the error scores of the cortically blinded Subgroup IIIb and the peripherally blinded Subgroup IIb for the open maze which was their first problem:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIb (Peripherally blinded)	Open maze, first	280.64 $\pm$ 53.55	225.54 $\pm$ 107.14
IIIb (Cortically blinded)	Open maze, first	506.18 $\pm$ 92.80	

The cortically blinded made significantly more errors than the peripherally blinded in the same maze. The former group also took more trials than the latter. The only exception to the general tendency is the time score, to which we cannot give much weight. The average retardation of Subgroup IIIb amounts to 288.39 per cent, being much higher than the 215.80 per cent of Subgroup IIb. Four of the eleven rats of Subgroup IIIb, or 36.36 per cent, failed the open problem; in Subgroup IIb there were five failures among the eleven rats, the percentage being 45.45.

A similar situation exists in the scores of the cortically blinded Subgroup IIIa and the peripherally blinded Subgroup IIa for the open maze when this was their second problem (Table VI). We present their error scores in tabular form below:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIa (Peripherally blinded)	Open maze, second	196.91 $\pm$ 43.93	138.19 $\pm$ 70.31
IIIa (Cortically blinded)	Open maze, second	335.10 $\pm$ 54.90	

As compared with the peripherally blinded, animals deprived of visual cortex present a higher error score; their trial score is also higher. Here again the time score stands out as a conspicuous deviation from the general tendency. The cortically blinded show an average retardation of 287.10 per cent, a value fairly constant throughout the cortically blinded subgroups for both mazes. But this value is not much higher than the 271.87 per cent of the peripherally blinded Subgroup IIa for the same problem. One of the ten rats, or 10 per cent, of Subgroup IIIa, and three of the eleven, or 27.27 per cent, of Subgroup IIa, failed the open maze.

The combined retardation of the two cortically blinded Subgroups IIb and IIIa for the open maze is 287.74 per cent which is still significantly greater than the corresponding 243.83 per cent of the peripherally blinded Subgroups Ib and Ia. However, the combined percentage of failures of the cortically blinded is lower than that of the peripherally blinded, the ratio being 23.18 per cent to 36.36 per cent.

Summing up, from the facts set forth in the present section we see that the cortically blinded animals show a severe retardation in learning the inclosed maze, while the peripherally blinded are not retarded to any significant degree. Undoubtedly vision plays little part in the learning of this maze. We must, therefore, seek the explanation of the tremendous retardation of the cortically blinded in some other source than the defect of vision.

The above statement also holds for the open maze. This is especially true if we lay emphasis on the error scores. The greater retardation of the cortically blinded animals may have been (1) the effects of damage to other sensory areas of the cortex, as contended by Hunter; (2) the effects of disrupting the visual space system which may have been established before the cortical blinding; and finally (3) the effects of the disturbance of non-specific functions of the visual cortex. We shall take up the discussion of this matter in some detail later.

c. Probable Reasons for the Difference in Results between Inclosed and Open Mazes. As we have seen, the contrast between the peripherally and cortically blinded animals is less pronounced for the open maze than for the inclosed maze. This fact calls for explanation. We can only offer our view in a tentative way. After extirpation of the visual projection areas, the diencephalic and mesencephalic visual centers remain functional. Animals thus operated retain unquestionably some brightness and position vision, although the pattern vision is lost (details on preceding pages). This residual vision can be of little help in tracing the inclosed maze due to the "walled-in" condition of the apparatus. On the other hand, the open maze allows greater freedom for such residual vision to function. There is some evidence of its actual functioning in supplying directive cues for running the maze.

Thus, a cortically blinded animal in the open maze can avail itself of a group of helpful cues (e.g. direction of luminous areas in the room) which is not available to a similarly operated animal in the inclosed maze. This might have been the reason for the relatively better performance of the cortically blinded in the open maze and for the lessened contrast in maze efficiency between the cortically and peripherally blinded animals in it.

4. Effects of Combined Peripheral and Cortical Blinding

We had two groups of animals blinded both peripherally and cortically. It was our intention to test whether the removal of the eyes in addition to visual cortex would entail the same effects as the mere removal of the eyes with the brain left intact. We found that the peripheral blinding produced quite different effects under the two conditions. For convenience, we shall take up the effects on the two forms of maze performances separately:

a. Inclosed Maze. Table V gives the average scores of Subgroup IVa, both peripherally and cortically blinded, for the inclosed maze when this was run as the first problem. We tabulate below the error scores of this subgroup together with those of the peripherally blinded Subgroup IIa and the cortically blinded Subgroup IIIa for the same maze:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIa (Peripherally blinded)	Inclosed maze, first	120.45 $\pm$ 30.01	895.22 $\pm$ 193.23
IIIa (Cortically blinded)	Inclosed maze, first	581.30 $\pm$ 46.67	434.37 $\pm$ 198.79
IVa (Peripherally and Cortically blinded)	Inclosed maze, first	1,015.67 $\pm$ 190.89	

Animals blinded both peripherally and cortically made more errors in the inclosed maze than animals operated in either way alone. The time scores are in accord with this general tendency, but the trials scores show some slight inconsistencies. The average retardation of Subgroup IVa runs as high as 436.53 per cent, in contrast to the 4.18 per cent and the 267.18 per cent of Subgroups IIa and IIIa respectively. Four of nine animals, or

44.44 per cent, failed this maze; the corresponding values for Subgroups IIa and IIIa are 0.00 and 70.00 per cent respectively.

Subgroup IVb, blinded in both ways, ran the inclosed maze as the second problem. They were more retarded than animals blinded in only one way. We reproduce the error score of Subgroup IVb together with those of Subgroups IIb and IIIb blinded peripherally and cortically respectively:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIb (Peripherally blinded)	Inclosed maze, second	88.09 $\pm$ 21.90	433.79 $\pm$ 133.78
IIIb (Cortically blinded)	Inclosed maze, second	290.36 $\pm$ 41.14	231.52 $\pm$ 139.97
IVb (Peripherally and Cortically blinded)	Inclosed maze, second	521.88 $\pm$ 131.98	

Subgroup IVb made more errors in the inclosed maze than either of the other subgroups. They also spent more time and took more trials in this maze than animals operated in either way alone. The average retardation of Subgroup IVb is 457.38 per cent, as against the 35.54 per cent and the 189.65 per cent of Subgroups IIb and IIIb respectively. One of the eight animals, or 12.50 per cent, failed this maze; the corresponding values for Subgroups IIb and IIIb are no higher than 0.00 and 9.09 respectively.

The combined retardation of Subgroups IVa and IVb for the inclosed maze is 446.95 per cent, in contrast to the 19.86 per cent of the peripherally blinded Subgroups IIa and IIb, and the 228.41 per cent of the cortically blinded Subgroups IIIa and IIIb for the same maze. The combined percentage of failures is 28.47, as against the perfect record of the two peripherally blinded subgroups and against the combined percentage of 39.54 of the two cortically blinded subgroups.

We have seen before that the mere loss of eyes has but little effect on the inclosed maze performance, but their loss in addition to the destruction of the visual cortex results in very serious retardation. The effect of peripheral blinding is thus seen to be dependent upon the working condition of the cerebral mechanism.

Moreover, the tremendous deterioration after the combined operation proves the actual functioning of the residual vision in maze running in the cortically blinded animals, though vision is not necessary for it in normals. The visual cues which are dispensable in animals with normal brain become very important for animals whose cerebral mechanism is running at a low efficiency level.

b. Open Maze. A similar situation manifests itself in the records for the open maze of animals blinded in both ways (Table VI). We compare the error scores of Subgroup IVb with combined operation, which first ran the open maze, with those similar records of the peripherally blinded Subgroup IIb and the cortically blinded Subgroup IIIb for the same maze:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIb (Peripherally blinded)	Open maze, first	280.64 $\pm$ 53.55	772.86 $\pm$ 138.06
IIIb (Cortically blinded)	Open maze, first	506.18 $\pm$ 92.80	547.32 $\pm$ 166.35
IVb (Peripherally and Cortically blinded)	Open maze, first	1,053.50 $\pm$ 127.25	

Animals with combined operation made more errors in the open maze than animals with single operation. The trial scores show the same trend, but some inconsistencies are present in the time scores. The average retardation of Subgroup IVb is 609.03 per cent, in outstanding contrast to the corresponding values of 215.80 per cent for Subgroup IIb and the 288.39 per cent for Subgroup IIIb. The group record is one of straight failures, not a single case of complete learning in the whole group; whereas the percentage failures of Subgroups IIb and IIIb are no higher than 45.45 and 36.36 respectively.

We now turn to the records of Subgroup IVa, blinded in both ways, which ran the open maze as the second problem. They were by far inferior to Subgroups IIa and IIIa, peripherally and cortically blinded respectively. They made more errors than the latter two subgroups as shown on following page:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIa (Peripherally blinded)	Open maze, second	196.91 $\pm$ 43.93	625.53 $\pm$ 110.66
IIIa (Cortically blinded)	Open maze, second	335.10 $\pm$ 54.90	487.34 $\pm$ 115.02
IVa (Peripherally and Cortically blinded)	Open maze, second	822.44 $\pm$ 101.07	

The trials scores are in accord with this general tendency; the time scores are again inconsistent. The average retardation of Subgroup IVa amounts to 797.27 per cent, as against the 271.87 per cent of Subgroup IIa and the 287.10 per cent of the Subgroup IIIa. Indeed, it represents the highest retardation ever suffered by any single subgroup. Eight of the nine animals, or 88.88 per cent, failed the open maze within time limit; while the percentage failures of Subgroups IIa and IIIa are only 27.27 and 10.00 respectively.

The combined retardation for the open maze of the two doubly blinded Subgroups IVb and IVa is 703.15 per cent which is far above the 243.83 per cent of the two peripherally blinded subgroups IIb and IIa and the 287.74 per cent of the two cortically blinded Subgroups IIIb and IIIa. The doubly blinded subgroups show a combined percentage failure of 94.44, while the corresponding percentages of the peripherally blinded subgroups and the cortically blinded subgroups are 36.36 and 23.18 respectively.

Enucleation of the eyes results in tremendous loss of efficiency in the open-maze habit; the same operation in animals deprived of visual cortex produces an extraordinarily serious deterioration. The effect of peripherally blinding is shown once more to vary with the working condition of the cerebral mechanism. That vision is functioning very actively in tracing the open maze in the cortically blinded is also evident from the effect of eliminating their residual vision.

5. *Summary of Experimental Results*

Illustrating more concretely the relative difficulty of the mazes and the relative effects of blinding, single and combined, the com-

bined percentages of failures in the animal groups for the two mazes are represented by the horizontal bars in Figure 3. The length of the bars is proportional to the size of the combined percentages in the various groups. The combined percentages for the inclosed maze is represented by continuous lines; those for the open maze, by broken lines. For the same purpose, the combined

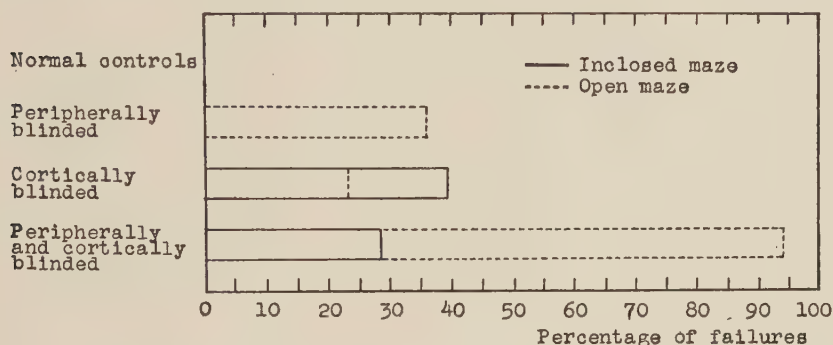


FIG. 3. HISTOGRAM OF THE COMBINED PERCENTAGES OF FAILURES IN THE ANIMAL GROUPS FOR THE TWO MAZE PROBLEMS

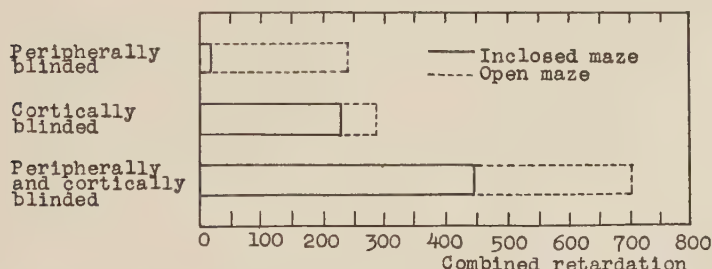


FIG. 4. HISTOGRAM OF THE COMBINED RETARDATIONS OF THE DIFFERENTLY BLINDED ANIMAL GROUPS IN THE TWO MAZE PERFORMANCES

retardations of the differently operated animal groups in the two maze habits are similarly diagramed by the horizontal bars in Figure 4. The length of the bars is proportional to the degree of retardation of the animal groups in terms of the percentage of the normal scores for the same problems.

We have given here the scores based upon the average percentage scores of the three criteria, time, errors and trials, in order to

take into account the various unknown factors in learning represented by each. Of these the error scores are most reliable and we have stressed them in the preceding discussions. Whether we use the error scores or the combined scores the trend of the results is the same. The trial scores also show the same general trend. The time scores are more often inconsistent, but where they seem to contradict the implications of other criteria, they are generally statistically unreliable.

Let us sum up the main points of our experimental results in a few lines. Animals with normal vision invariably make better records in the open than in the inclosed maze. On the other hand, animals deprived of the eyes are at a conspicuous disadvantage in the open maze. The open maze habit normally involves vision to a great extent. Cortical blinding is generally more disturbing for maze learning than extirpation of the eyes. The contrast is more pronounced in the inclosed than in the open maze where the residual vision after cortical operation plays a larger part. The combination of peripheral and cortical blinding produces more severe retardation than either one alone.

Since the cortical operations involved somewhat more than the area striata, we must consider the effects of this additional destruction before attempting to interpret the data.

6. Possible Influences of Additional Subcortical and Non-striate Cortical Lesions on Learning Scores

The first question to be settled in relation to our data concerns the possible effects of lesions involving non-visual areas of the cortex. Hunter ('30) has interpreted Lashley's data on the correlation between extent of lesion and retardation as due to the involvement of more than one sensory field in the larger lesions. It is absolutely necessary to control our results as to the possible influences of additional non-striate cortical and subcortical injuries.

a. Anatomical Topographical Relations of the Non-striate Cortical Areas Frequently Involved in the Operations. Recent work indicates that the extent of the area striata is somewhat less than that implied in Fortuyn's diagram (Volkman, '26; Lashley, '34b).

Anteriorly it begins at about level 19 of Fig. 2 and extends to the caudal pole of the hemisphere. The medial border corresponds pretty closely with the edge of field w, but the area is only two thirds the width shown in the diagram, so the lateral border should lie farther to the right.

The adjacent sensory projection areas are probably those of audition, olfaction and general sensation. Lesions in the lower part of field p are followed by retrograde degeneration in the medial geniculate body, indicating in conformity with Wiley's experiments ('32) that this region has auditory functions. Between this field and the area striata there is a zone, at least as broad as the latter, injury to which results in no thalamic degeneration. In front of the area striata is a zone, extending from about levels 9 to 14, lesion to which is followed by degeneration of the lateral thalamic nucleus. Between it and the area striata there is also an area of non-sensory cortex. Medial to the area striata, the cortex, i.e., the supposed visual association areas, m', and aa, is in close association with the hippocampal structures and is probably olfactory in function. The studies of Swann ('34) show that olfactory discrimination is not disturbed by destruction of this zone or of the dorsal convexity of the hippocampus. It is thus evident that lesions which exceed the limits of the area striata by a considerable extent (2 mm. or more) do not invade any other cortical fields which are primarily sensory. Lashley and Frank ('34c) have shown that destruction of any region adjacent to the striate cortex and of any part of this field itself do not seriously disturb retention of habits based on pattern vision, so long as some part of the binocular projection field remains intact. Such results indicate that trophic disturbances sufficient to interfere with the function of sensory fields are not usually produced by lesions adjacent to the fields.

We have attempted to destroy completely the visual parts of the cortex, projection as well as "association" areas, that is, fields w and m' and aa. When our work was begun, fields m' and aa were still regarded as visual associational and were thereupon destroyed intentionally. This explains the rather constant involvement of these areas in the inflicted lesions. For conven-

ience, we still call them visual associational in the following discussions. The cortical field next most involved is area p, owing to its topographical contiguity to area w and to the difficulty of controlling the depth which the thermo-cautery goes in destroying the latero-caudal part of area w. The caudal points of fields f, f' and n (motor), antero-medial to area w, and the dorso-caudal wedge of field j (somesthetic), antero-lateral to area w, are also frequently involved, but the injuries rarely amount to any important proportions.

The thermo-cautery is not a satisfactory instrument for inflicting injury to a limited spot; a greater or less involvement of the dorsal convexity of hippocampus is hard to avoid, as the visual cortex is the thinnest part of the whole neo-pallium. In some cases with extensive injuries the lateral geniculate body, the anterior nucleus of thalamus, or the superior colliculus (in very few cases, also the inferior colliculus) of the midbrain is involved. These non-visual parts of the cortex and the subcortical tissues might have something to do with maze performance. We shall try to control the effects of the strictly visual striate lesions in comparison with the possible influences of subcortical injuries and of various non-striate cortical lesions taken as a whole and separately.

b. Possible Influences of Subcortical Injuries. Table VIII presents a comparison of the error scores of animals with and without additional subcortical lesions for the inclosed and open mazes which were run as their first problems. The reason for the selection of the error scores for separate treatment is their generally acknowledged high consistency and reliability as an index of maze efficiency, as discussed in a former section. The conditions of the learning of the first maze are also unquestionably simpler as compared with those of the second problem. From Table VIII we see that the differences between the cases with and without subcortical lesions are not constant. Where the former make poorer scores in the inclosed maze the differences are insignificant in comparison with the inferiority of both groups to the peripherally blinded animals (see Table V). Moreover, the cortical lesions in the animals with subcortical injuries are greater than in the others

TABLE VIII
Comparison of the Error Scores of Animals with and without Subcortical Lesions in Addition to the Destruction of the Visual Cortex for the Inclosed and Open Mazes Which Were Their First Problems

Subgroups IIIa and IIIb were cortically blinded; subgroups IVa and IVb were both peripherally and cortically blinded. Under "effect," the apparently positive (+) or negative (-) influence of the additional subcortical lesions upon the error score is presented.

core is presented.

ANIMAL GROUP	KIND OF LESION	WITH SUBCORTICAL LESION			WITHOUT SUBCORTICAL LESION			EFFECT	
		Cases (Experimental Number)	Number of Cases	Average Percentage Lesion	Average Error Score	Number of Cases	Average Percentage Lesion		Average Error Score
Inclosed Maze									
IIIa	Thalamic Mesencephalic Hippocampal: Light	75, 80 73, 75, 77, 80, 82	2 5	29.5 27.5	620.00 538.60	8 5	23.5 22.2	571.63 624.00	+ -
	Extensive	6, 18, 59, 62, 77, 82	6	25.0	584.00	2 (Nos. 2, 73)	19.7	534.50	+
IVa	Extensive	75, 80	2	29.5	620.00				
	Thalamic Mesencephalic Hippocampal: Light	22, 23, 90 1, 90	3 2	34.4 26.6	1,401.66 1,302.00	6 7	28.6 34.2	822.67 933.86	+ +
	Extensive	3, 50, 64, 85 20, 22, 23, 90	4 4	29.4 34.6	1,037.75 1,182.25	1 (No. 1)	19.1	261.00	+
Open Maze									
IIIb	Thalamic Mesencephalic Hippocampal: Light	14, 87 17, 68, 84	2 3	31.3 21.8	510.50 248.33	9 8	24.4 27.1	505.22 602.88	+ -
	Extensive	14, 17, 68, 79, 83, 84	6	25.3	310.83	3 (Nos. 7, 15, 16)	22.1	997.00	-
IVb	Extensive	21, 87	2	31.9	356.00				
	Thalamic Mesencephalic Hippocampal: Light	12, 65, 67 65, 66, 67	3 3	31.3 30.2	908.00 1,082.33	5 5	29.0 29.6	1,140.80 1,036.20	- +
	Extensive	4, 13, 66, 69 12, 65, 67	4 3	30.9 31.3	1,340.25 908.00	1 (No. 89)	21.5	343.00	+

(Table VIII) and this fact alone is sufficient to account for the greater retardation.

Lashley ('29, '33b) has attempted to estimate the possible influences of the subcortical lesions on the maze learning in various ways. He has never found that the inclusion of cases with thalamic or hippocampal lesions in the whole series alters significantly the results from those which would have been obtained if only cases with neo-palliate lesions were included in the computation of the constants. This is in general true of our results. We may substitute the average error score of the cases within a subgroup either with or without such subcortical lesions for the error score of the whole subgroup without altering the rank of this subgroup among the normal and operated subgroups for the same problem. For instance, taking the cortically blinded Subgroup IIIa in the inclosed maze (Table VIII), there have been computed six error scores (the two scores for the hippocampal cases are averaged together) for the three different groupings with and without a certain kind of subcortical lesion: viz., 620.00 vs. 571.63; 538.60 vs. 624.00; 602.00 vs. 534.50. Any one of these scores may be substituted for the score of the whole subgroup 581.30 without affecting the rank of Subgroup IIIa as intermediate between the peripherally blinded Subgroup IIa and the peripherally and cortically blinded Subgroup IVa in the matter of errors in learning the same maze. The same is true of the error scores of other animal groups for the maze problems. Exceptions are the error scores of the two cases without any hippocampal injury in Subgroups IVa and IVb for the inclosed and open mazes respectively. Since there is only one animal in each case, no importance should be given. The additional subcortical lesions do not seem to influence the group error scores in any specific way.

c. Possible Influences of Non-Striate Lesions Taken as a Whole. In an attempt to destroy completely the visual cortex, the visual association areas m' and aa, the dorsal edge of the auditory area, p, the dorso-caudal part of the somesthetic area j, the caudal parts of the motor areas f, f', and n, were rather frequently involved in the cortically operated animals. This is especially true of the supposed visual association areas which were destroyed

intentionally. It is practically not feasible to separate the cases with from those without extra-striate injuries in the regular animal groups and determine the possible effects of these injuries upon the learning scores. However, we can determine the possible influences of extra-striate lesions by comparing the scores for the inclosed maze of Subgroup IIIa and Group V. The former was with such extra-striate lesions, while the latter was practically not (details in a later section). Subgroup IIIa made naturally more errors than Group V, the ratio being 581.30 to 317.62. The group average retardations are 267.18 and 221.11 respectively. Though cortically blinded only partially, Group V was by far inferior to the peripherally blinded Subgroup IIa for the same problem. The latter made an error score of 120.45, with an average retardation of 4.18. The control Group V may well be substituted for the regular Subgroup IIIa without altering the rank of the cortically blinded animals as intermediate between the peripherally blinded Subgroup IIa and the both peripherally and cortically blinded Subgroup IVa. The additional involvement of the extra-striate fields taken as a whole is thus seen to exert no special influence on the group score.

d. Possible Influences of Non-Striate Lesions Taken Separately. It has occurred very rarely that a single non-striate cortical field is involved with the destruction of the area striata. Therefore, it is difficult to estimate the possible influences of separate non-striate cortical fields involved. We have divided the animals in each of the cortically operated subgroups into classes according to the non-striate field most involved in addition to the destruction of the area striata. The area of this main additional lesion in each case was measured and expressed as a percentage of the total area of the cerebral cortex. We have computed the average percentage lesion, together with the average error score, for each class. In this way we hope to get some insight into the relative influences of the additional lesions to different non-striate fields upon the class error scores. We are fully aware that the destruction of area striata and the lesser involvements of other non-striate areas than the one in question are not quite uniform in all cases. Table IX presents such a comparison of the class error

TABLE IX
Comparison of the Error Scores of Animals with Additional Injuries to the Various Cortical Fields Besides the Destruction of the Visual Areas for the Inclosed and Open Mazes Which Were Their First Problems

Subgroups IIIa and IIIb were cortically blinded; Subgroups IVa and IVb were both peripherally and cortically blinded. N means the number of cases; M, the mean of the percentage lesions and the mean of the error scores of a special class with a definite non-visual area as the next most involved cortical field. Under "effect" the apparently comparative influences of the additional involvement of the various non-visual fields are indicated.

ANIMAL GROUP	AREAS m'aa (VISUAL ASSOCIATION)			AREA p (AUDITORY)			AREA j (SOMESTHETIC)			EFFECT
	Number	Percentage Lesion	Error Score	Number	Percentage Lesion	Error Score	Number	Percentage Lesion	Error Score	
Inclosed Maze										
IIIa	6	5.1	885	2	5.8	597	59	2.5	978	j > m'aa > p
	62	4.9	281	18	6.0	379	N = 1	M = 2.5	M = 978.0	
	73	3.8	472		M = 5.9	M = 488.0				
	75	4.3	604							
	77	5.7	671							
IVa	80	6.0	636							p > m'aa
	82	5.5	310							
	N = 7	M = 5.0	M = 551.3							
	1	5.0	261	3	5.5	2,725				
	50	5.7	350	20	7.9	524				
IIIb	64	5.7	446	22	7.2	1,107				m'aa > p
	85	6.0	630	23	8.9	755				
	90	6.0	2,343							
	N = 5	M = 5.7	M = 806.0		M = 7.4	M = 1,277.8				
Open Maze										
IIIb	15	2.8	1,780	7	7.4	489				m'aa > p
	16	3.8	722	14	7.0	810				
	68	3.8	250	17	5.1	247				
	83	5.3	166	21	7.7	501				
	84	6.0	248	79	6.8	144				
IVb	N = 5	M = 4.3	M = 633.2	87	5.1	211				p > m'aa
				N = 6	M = 6.5	M = 400.3				
	12	6.0	1,122	4	7.8	2,117				
	13	6.0	897	66	7.4	1,645				
	65	6.0	886	67	6.8	716				
IVb	89	5.7	343	69	7.0	702				p > m'aa
	N = 4	M = 5.9	M = 812.0	N = 4	M = 7.3	M = 1,295.0				

scores of the cortically operated subgroups with different chief involvements of the non-striate areas for both mazes which were run as their first problems. With the cortically blinded animals in the inclosed maze, Subgroup IIIa, somesthetic injuries have the greatest influence, although there is only one case in this class; then come the effects of visual association and auditory lesions. With the peripherally and cortically blinded animals in the same maze, Subgroup IVa, the lesions to auditory areas seem to be more influential than those to the visual association areas. This relation is reversed in the relative effects of injuries to auditory and visual association areas with the cortically blinded animals in the open maze, Subgroup IIIb. The auditory lesions are again more influential than the injuries to the visual association areas as judged from the scores of the two classes of the peripherally and cortically blinded Subgroup IVb for the open problem. The relative influence of any main additional non-striate lesion is not at all constant as compared with those of other similar involvements.

The data here presented may be viewed from another angle. The average error score of any class may be substituted for the error score of the subgroup without affecting the position of this subgroup in the error score rankings of the different animal subgroups. For instance, either of the three class error scores of the cortically blinded Subgroup IIIa for the inclosed maze, 551.3, 488.0, and 978.0, may replace the group error score 581.3 and this subgroup still retains its rank between the peripherally blinded Subgroup IIa and the both peripherally and cortically blinded Subgroup IVa. This is generally true of all class error scores of other subgroups for the two mazes. At any rate, our data have not revealed any special distortions of the group error scores by any kind of additional non-striate lesions.

From the controls instituted in the foregoing pages it should be clear that the inclusion of cases with various subcortical lesions or non-striate cortical injuries in computing the constants does not affect significantly the group error scores in any specific direction. In short, the deterioration in the learning ability of the cortically operated groups is mainly the consequence of the removal of the visual cortex.

7. *Some Related Findings*

Before attempting an interpretation of our results we shall turn very briefly to some related findings that have come out in the experimental elaboration of our main theme, even at the risk of some repetition. These accidental findings shed light upon some allied problems and give a hint to the interpretation of our results.

a. Effects of Sense Privation versus Cortical Lesion. Concerning the relative effects of peripheral sense privation and corresponding cortical lesion, the question discussed by Hunter and Lashley, our results are unequivocal in proving that cortical lesion is by far more detrimental. We shall reiterate our findings relevant to this question. Peripheral privation of vision by enucleation of the eyes affects little, if any, the inclosed maze scores; but the extirpation of the visual cortex, even partial, provokes a tremendous retardation (Group V). This is also true of the open maze habit, but to a lesser degree for reasons set forth in the foregoing pages. We shall see presently that the deterioration following the destruction of the visual projection areas is inexplicable by the mere loss of the visual function, for the visual cues are not necessary in the learning of at least the inclosed maze. The detrimental effect must have resulted from the disturbance of some basal function other than visual reception which is much more important for maze efficiency than the visual cues. With the destruction of the visual areas, the loss which counts more is not sensory, but more general. In other words, cortical blinding means loss of this general function as well as that of visual reception. This explains why the cortical lesion to the visual areas is more detrimental than the corresponding peripheral sense privation.

b. Behavior Differences between Normal, Peripherally and Cortically Blinded Animals. Apart from the three criteria of learning, trials taken, time spent and errors made, as adopted in the present study, there is another significant criterion, the quality of the maze performance, of which we are still in need of a convenient standard of judgment. The difference in maze behavior of the

normals and the peripherally blinded was hardly noticeable in the inclosed maze; while in the open form the blind animals made more but somewhat reasonable random movements. The cortically operated behaved quite differently from both the normals and the peripherally blinded. Even when they made fairly good learning scores the quality of their work was decidedly inferior to that of the normal controls and the peripherally blinded animals, especially at the initial stage of learning. The cortically operated, even those with only a lesser lesion in the area striata, more frequently wasted their time in the starting box or platform; entered a blind runway repeatedly; ran a straight course in the maze, usually the first three sections; retraced from a particular section of the maze to some other section and repeated this error many times; took some blind runways as regular parts of the pathway to the food; rubbed their sides against the maze-wall at definite spots; or finally, dashed into a certain blind alley and fell asleep, giving up the task entirely. Defaecation and urination in the open maze were other features in the cortically operated. Generally speaking, the differences in maze behavior of the animal groups were more pronounced in the open than in the inclosed maze.

These behavior differences in maze performance, though not capable of quantitative statement at present, are exceedingly important, as they shed light on the way in which the cortical lesion influences the maze efficiency. In a word, the behavior peculiarities of the cortically operated animals are nothing short of symptoms of general dementia, i.e., the defective functioning of the cerebral integrating machine.

INTERPRETATION AND DISCUSSION

Enough evidence has been cited in the foregoing pages to show that the destruction of the visual cortex is more detrimental than the removal of the eyes. And this is generally true for both the inclosed and the open maze habits. It is firmly established in the higher mammals that the visual area is the most specialized of all sensory projection areas of the cortex; a point-to-point correspondence has been found between the retinal quadrants and

the visual projection parts in the occipital lobes. The afferent visual system from the retinal beginnings to the cortical terminations is "spatially" organized according to the principle of localization. The same may be said of the visual system in the rat according to Lashley's most recent studies ('34). How can we account for the disproportionate retardation following the loss of the "cortical retinae" (Munk, '81), as compared with that following the removal of the peripheral retinae?

There seems to be three possible explanations, as stated in a preceding section. 1, the sensory loss other than visual; 2, the disturbance of visual organization other than the primary sensory functions; 3, the disturbance of some unknown and non-sensory function of the visual area which may correspond to the *action commune* of Flourens or the non-specific dynamic function of Lashley.

(1) Hunter ('30) interprets the greater defect after cerebral lesions as largely due to the involvement of other sensory areas than the one in question. In a former section we have instituted various controls for our data on the defects of cortical blinding as to the possible influences of additional non-striate lesions. We have treated the possible effects of additional non-striate involvements as a whole and separately. In no case have we found the additional injuries exerting any influence in a special direction. Among the cortically blinded groups, either that with or that without non-striate lesions may represent the whole without affecting its original rank among the normal and operated groups. The influence of any chief additional non-striate lesion is not constant in relation to other similar involvements. The average error score of some animals with a certain dominant non-striate lesion may replace the group score without altering the former place of the whole group in the rankings of the various groups of animals. Finally, it is doubtful that the lesions extending beyond the striate area invaded any other primary sensory area. We are, therefore, forced to attribute the greater retardation of the cortically operated mainly to the loss of visual areas, which constitute the greater part of the cortex involved in the lesions.

Turning once more to facts, our view is strongly supported by

the learning scores for the inclosed maze of the partially cortically blinded Group V (Tables III, V and VII). With this group the operation was limited within the area striata or approximately so, without subcortical lesion of any kind. We examined the condition of the non-visual thalamic nuclei for each case to check up any possible involvement of other non-visual cortical areas. All cases in which any of these nuclei showed signs of degeneration were accordingly discarded. In each of the thirteen cases in this group a considerable portion of the visual areas was undoubtedly left functional. Yet this group was far inferior to the peripherally blinded Subgroup IIa in maze efficiency. We reproduce their error scores below:

SUBGROUP	PROBLEM	ERROR SCORE	DIFFERENCE
IIa (Peripherally blinded)	Inclosed maze, first	120.45 $\pm$ 30.01	197.17 $\pm$ 47.41
V (Partially cortically blinded)	Inclosed maze, only	317.62 $\pm$ 36.70	

Group V, though cortically blinded only partially, made much more errors than the total blind Subgroup IIa. The former also spent more time and took more trials than the latter. The percentage retardations of Group V for the three criteria of learning are fairly constant, a little more than two hundred per cent, with an average retardation of 221.11 per cent, as against the 4.18 per cent of Subgroup IIa. In other words, partially cortically blinded animals are fifty-two times poorer than the peripherally blinded in the same maze. Subgroup IIa made a record of straight success, but the percentage failure of Group V ran as high as 61.54. It seems safe, then, to state that the loss of the visual areas is chiefly responsible for the greater retardation of the cortically blinded animals.

(2) Granted that the extirpation of visual areas entails a greater retardation in the cortically blinded, this fact might still be interpreted as due to sensory disturbance. We started to train our animals at an adult age. It is quite possible that our animals may have developed a spatial organization in visual terms (visual

imagery, if you will). This organization, if present, may survive the loss of eyes and be still functional in maze learning of animals peripherally blinded. Interference with this space system consequent to the destruction of area striata and cortical tissues adjacent to it may affect the maze performance. In such a case, the loss after extirpation of visual cortex would be visual, though not primarily sensory.

This interpretation may be dismissed on experimental grounds. In another experiment just concluded, that is, the third step in our experimental procedure mentioned at the beginning of the present report, we employed animals blinded in infancy before the eyes opened naturally. The visual cortex was thus prevented from functioning visually from birth. The animals thus blinded were not very inferior to the normal controls in the acquisition of the inclosed maze habit and retained the habit very well after a period of two weeks. On the other hand, those animals with additional lesions to the visual cortex learned the maze with difficulty, if at all; and lost the habit heavily after the additional operation, in case the maze had been learned before. The poor scores of these animals cannot be interpreted as due to the loss of the visual function of the visual cortex, as it had never been functioning in a visual way. This constitutes a more decisive proof of the non-visual function of the visual cortex. Since we shall report this experiment in a separate paper, suffice it to mention the main points of our results.

(3) The only alternative left is to attribute the greater retardation after cortical operation to the loss of some non-sensory function of the visual areas. As stated at the formulation of this research program, if the function of the visual areas is purely sensory, as the literary expression "cortical retinae" implies, the loss in maze efficiency after cortical blinding should be comparable to that following peripheral blinding. We found that peripheral blinding has but little influence on the maze performance, especially the inclosed type, while cortical blinding produces much greater retardation than the peripheral operation. The serious deterioration of the cortically blinded is certainly not explicable as merely due to the elimination of the cortical sensory

reception as such. Granted that the visual areas function exactly as "cortical retinae," in the same sense as the peripheral retinae; then their partial destruction means naturally partial blinding. We are reasonably justified in expecting less retarding effect of the partial than the total blinding. But as a matter of fact, the partially cortically blinded Group V was found fifty-two times poorer than the totally peripherally blinded Subgroup IIa in the inclosed maze. On the purely sensory view of the functions of the visual areas, we would be forced to the absurd position of maintaining that partial blinding has even greater retarding influence than total blinding.

The evidence thus seems to preclude a sensory loss, either at a primary receptive or perceptual level, as an explanation of the inferiority of animals with cortical lesions. What the additional function of the striate area may be, which is responsible for the better performance of blind animals with the area intact, is still obscure. The results of our later experiment with blinding in infancy indicate that the function disturbed is not one acquired as a result of visual experience. It may be that the striate area has some innate specific function concerned with the organization of spatial habits and that this specific function is destroyed in the cortically blinded cases. The alternative to such a mysterious function would seem to be some general facilitative function common to this and other areas of the cortex. The results of Lashley ('29) and of Lashley and Wiley ('33b) indicating that a similar condition prevails in each of the sensory fields of the cortex lend strong support to the latter interpretation.

As we see it, the visual areas are normally participating in the integrative activities of the cerebrum as a whole. In the cortically blinded animals, along with the privation of the "cortical retinae," the smooth working of the total neural mechanism is disturbed. It runs at a low ebb and no longer functions in a unitary way, which is required for an efficient maze learning. The operation is local, but its effects are general. Animals thus operated present a picture of dementia. We have some factual support for this statement on the behavior side. With an intact brain, peripherally blinded animals behave as well as the normals

in the maze. On the other hand, the cortically operated, even with comparatively light lesions and with the residual visual tissues still functional, betray many behavior peculiarities as enumerated in a preceding section. Enucleation of the eyes results merely in visual anesthesia, while the removal of the visual cortex means general dementia as well. The cerebral integrating mechanism can never function normally in a unitary way without the participation of its visual parts. The function of the visual cortex in this connection is certainly non-visual.

This more dynamic concept of the function of the visual cortex has some parallels in the literature. Munk ('81, '09) produced "psychic blindness" in the dog by inflicting a slight injury to what he called the "cortical retina." Goltz ('81) reinterpreted his results and ascribed them to the "visual weakness" and dementia of the animals. Munk himself noticed that the cortically blinded dog lost orientation to his environment; while the peripherally blinded got readily accustomed to the new situation. Luciani and Seppili ('86) provoked partial psychic blindness in the dog with occipital lesion; the dog reacted to food but failed to distinguish it from other things. Minkowski ('11) extirpated both striate areas in the dog; the resulting disturbance of orientation was far more severe than that in the peripherally blinded animal.

The studies on aphasic defects of Marie, Moutier, Head and others point to the fact that apart from the sensory defects associated with lesions to definite cortical areas, the general intelligence of the subjects suffers even more profoundly. Among the chief symptoms of occipital gun-shot wounds analysed by Poppelreuter ('17, '23), Fuchs ('20, '21) and Goldstein and Gelb ('20) is the hypofunction of "attention." It expresses itself in the inability to count objects visually; in the difficulty in searching for something in the field of vision; in the reduced number of objects grasped at a single glance; in the over-estimation of time interval; in the disturbance of cutaneous localization, and in various other ways. Another notable symptom of occipital lesions is the disturbance of "recognition" or "memory" in general. Poppelreuter found the process of recognition in his

patients much slowed down. Heidenhain ('27) and others reported cases who could identify simple familiar things, but not complex ones. Their pattern vision was good enough for perceiving forms, but they were unable to name objects. Here the difficulty lies in the incapability to translate visual impression into verbal terms. The occipital cases are generally unable to interpret visual figures unless more details are given. Poppelreuter is of the opinion that the defect is not merely the loss of visual memory as such but really the inability to see the relations between the separate parts. From his extensive studies of cases of occipital lesions Goldstein ('24) has come to the conclusion that while isolated disturbances of simple sensory functions may occur, there is always some involvement of the entire cerebral mechanism.

We are then forced to conclude that the visually specialized cortical areas have some general function,—an *action commune* in addition to their *action propre*, in the terminology of Flourens. This is a further confirmation of Lashley's analysis that "not only is there diversity in the modes of action of different parts of the cortex but a single area, highly specialized and differentiated for one activity may be wholly undifferentiated with respect to another in which it also participates." (Lashley, '31c). This general function, perhaps common to all specialized cortical areas, is probably instrumental in bringing about the unitary functioning of the brain as a whole.

Another point waits for some comment. The dispensability of vision for the inclosed maze is by no means absolute. It is unnecessary for animals with normal brains, but not for those with a brain deprived of the visual areas. How can we account for the different rôles which vision plays in the two cases? There seems to be only one possible explanation. First, the removal of the eyes has no influence on the learning of the inclosed maze. If visual cues are normally used the blind animals have no difficulty in falling back upon the non-visual cues. As pointed out by Lashley ('29) the sensory elements of the maze habit may have an alternative function, so that the elimination of one sensory system would be followed by the performance of the habit through

the use of other undisturbed sensory cues. With the open maze habit this transfer cannot be effected without much loss of efficiency. Second, the destruction of the visual cortex has serious influences on learning. As demonstrated before, this cannot be the consequences of the abolition of a sensory function, since vision is not necessary for learning the maze at normal rate. The detrimental effect in this case is primarily due to interference with the functional efficiency of the rest of the nervous system or to the defect of the associative mechanism. Third, the elimination of the eyes in animals with injuries to the striate areas produces additional retardation, although it has little or no effect on animals with normal brains. In all probability, animals with striate lesions still use some brightness cues: the loss of eyes leaves them without these cues and they somehow have greater difficulty in falling back upon non-visual cues. The visual areas normally participate in the general integrative activity of the cerebrum; with their privation the cerebral mechanism ceases to be an unitarily functioning affair. It loses much of its function as an agent to adjust different nervous processes to do a certain task, thus unifying the bodily functions. With the mutilated integrating mechanism an alternation of the sensory components can no longer be readily effected, as in the case of animals with normal brains. In other words, the greater difficulty of readjusting the sensory components of the maze habit in cortically operated animals is to be attributed to the mutilation of the cerebral integrative function, that is, to general dementia.

SUMMARY AND CONCLUSIONS

Animal groups, normal, blinded peripherally, cortically and in both ways have been trained in inclosed and open mazes of the same pattern with the following results.

1. The open maze is easier than the inclosed for normals and possibly for the cortically blinded, but more difficult for the total blinds whether or not with additional cortical blinding.
2. The removal of the eyes has little or no influence on the learning of the inclosed maze, but has tremendous effect on the learning of the open maze.

3. The destruction of the visual projection areas is more detrimental than the removal of the eyes. Cortical lesion is more detrimental than the corresponding peripheral sense privation. This is true for both forms of the maze.

4. After the destruction of the visual areas the animals still retain some position and brightness vision, but the pattern vision is all gone.

5. The residual vision is more important for the learning of the inclosed maze by the cortically blinded animals than is the case with normal controls.

6. In the absence of pattern vision in the cortically blinded animals, the residual vision seems to be able to supply visual cues for the general orientation and consequently for the better performance in the open maze.

7. Peripheral blinding when combined with cortical blinding produces further retardation, the effect being greater in the open than in the inclosed maze habit.

8. The additional retardation, just mentioned, is explicable by the greater difficulty in falling upon non-visual cues than is the case with the peripherally blinded animals with normal brains; this in turn is due to the defective cerebral integration.

9. Vision always plays a greater rôle in the open than in the inclosed maze habit, irrespective of the working condition of the cerebral mechanism.

10. The quality of maze performance of the cortically blinded is inferior to that of the peripherally blinded and the normals, suggesting dementia in the cortically operated.

11. The visual projection areas normally participate in the integrative activity of the cerebrum as a whole; that is, in addition to their primary function of visual reception, they still have some sort of a general function.

BIBLIOGRAPHY

- FLOURENS, P. 1842. *Researches expérimentales sur les propriétés et les fonctions du système nerveux*. Paris.
- FORTUYN, D. 1914. "On the Cell Laminations of the Cerebral Cortex in Some Rodents," *Mott's Archives of Neurology*, vi, 221-354.
- FUCHS, W. 1920. "Untersuchungen über das Sehen der Hemianopiker und

- Hemiambyopiker. II. Die totalisierende Gestaltauffassung," *Zeit. f. Psychol.*, lxxxvi, 1-143.
- FUCHS, W. 1921. "Eine Pseudofovea bei Hemianopikern," *Psychol. Forsch.*, i, 157-190.
- GELB, A. UND GOLDSTEIN, K. 1920. *Psychologische Analysen hirnpathologischer Fälle*. Leipzig.
- GOLDSTEIN, K. 1924. "Das Wesen der amnestischen Aphasie," *Schweiz. Arch. f. Neurol. u. Psychiat.*, xv, 163-175.
- GOLTZ, F. 1881. *Über die Verrichtungen des Grosshirns*. Bonn.
- HEIDENHAIN, A. 1927. "Beitrag zur Kenntnis der Seelenblindheit," *Monatschr. f. Psychiat. u. Neurol.*, lxvi, 61-116.
- HERRICK, C. J. 1926. *Brains of Rats and Men*. University of Chicago Press.
- HUNTER, W. S. 1929. "The Sensory Control of the Maze Habit in the White Rat," *J. Genet. Psychol.*, xxxvi, 505-537.
- 1930. "A Consideration of Lashley's Theory of Equipotentiality of Cerebral Action," *J. Gen. Psychol.*, iii, 455-468.
- 1931. "Lashley on 'Cerebral Control vs. Reflexology,'" *J. Gen. Psychol.*, v, 230-234.
- KLÜVER, H. 1927. "Visual Disturbances after Cerebral Lesions," *Psychol. Bull.*, xxiv, 316-358.
- LASHLEY, K. S. 1929. *Brain Mechanism and Intelligence*. University of Chicago Press.
- 1930. "The Mechanism of Vision: I. A Method for Rapid Analysis of Pattern Vision in the Rat," *J. Genet. Psychol.*, xxxvii, 453-460.
- 1931a. "The Mechanism of Vision: IV. The Cerebral Areas Necessary for Pattern Vision in the Rat," *J. Comp. Neur.*, liii, 419-478.
- 1931b. "Cerebral Control versus Reflexology. A Reply to Professor Hunter," *J. Gen. Psychol.*, v, 3-20.
- 1931c. "Mass Action in Cerebral Function," *Science*, lxxiii, No. 1888, 245-254.
- 1933a. "Integrative Function of the Cerebral Cortex," *Physiol. Rev.*, xiii, 1-42.
- LASHLEY, K. S. AND WILEY, L. E. 1933b. "Studies of Cerebral Function in Learning. IX. Mass Action in Relation to the Number of Elements in the Problem to be Learned," *J. Comp. Neur.*, lvii, 3-55.
- LASHLEY, K. S. 1934a. "The Mechanism of Vision. VII. The Projection of the Retina upon the Primary Optic Centers of the Rat," *J. Comp. Neur.*, lix, 341-373.
- 1934b. "The Mechanism of Vision. VIII. The Projection of the Retina upon the Cerebral Cortex of the Rat," *J. Comp. Neur.* (In press).
- LASHLEY, K. S. AND FRANK, M. 1934c. "The Mechanism of Vision. X. Post-operative Disturbances of Habits Based upon Detail Vision after Lesions in the Cerebral Visual Areas of the Rat," *J. Comp. Psychol.* (In press).
- LUCIANI, L. UND SEPPILI, G. 1886. *Die Function-Localisations auf der Grosshirnrinde*. (German translation by Fraenkel, Leipzig.)
- MILES, W. R. 1927. "The Narrow-Path Elevated Maze for Studying Rats," *Proc. So. for Exp. Biol. and Med.*, xxiv, 454-456.

- MILES, W. R. 1930. "The Comparative Learning of Rats on Elevated and Alley Mazes of Same Pattern," *J. Comp. Psychol.*, x, 237-261.
- MINKOWSKI, M. 1911. "Zur Physiologie der Sehsphäre," *Arch. f. d. Ges. Physiol.*, cxli, 171-327.
- MUNK, H. 1881. *Über die Funktionen der Grosshirnrinde*. Berlin.
- 1909. *Über die Funktionen von Hirn und Rückenmark*. Berlin.
- POPPELREUTER, W. 1917. *Die psychischen Schädigungen durch Kopfschuss*. Leipzig.
- 1923. "Zur Psychologie und Pathologie der optischen Wahrnehmung," *Zeit. f. d. ges. Neurol. u. Psychiat.*, lxxxiii, 26-152.
- RAMON Y CAJAL, S. 1911. *Histologie du système nerveux*. Vol. II. Paris.
- ROSE, M. 1929. "Cytoarchitektonischer Atlas der Grosshirnrinde der Maus," *J. f. Psychol. u. Neurol.*, Bd. 40, 1-51.
- SWANN, H. G. 1934. "The Function of the Brain in Olfaction. II. The Results of Destruction of Olfactory and Other Nervous Structures upon the Discrimination of Odors," *J. Comp. Neur.*, lix, 175-201.
- TOLMAN, E. C. AND NYSWANDER, D. B. 1921. "The Reliability and Validity of Maze Measures for Rats," *J. Comp. Psychol.*, vii, 425-460.
- VINCENT, S. B. 1912. "The Function of the Vibrissae in the Behavior of the White Rat," *Behavior Monographs*, Ser. No. 5.
- 1915. "The White Rat and the Maze Problem: III. The Introduction of a Tactual Control," *J. Animal Behavior*, v, 175-184.
- VOLKMANN, V. 1926. "Vergleichende Untersuchungen an der Rinde der 'motorischen' und 'Sehregion' von Nagetieren." *Anat. Anz., Ergänzungsheft*, Bd. 61, 234-243.
- WILEY, L. E. 1932. "The Function of the Brain in Audition," *J. Comp. Neur.*, liv, 109-141.

PLATES

DIAGRAMS OF THE EXTENT AND LOCUS OF THE CEREBRAL LESIONS IN EACH OF THE ANIMALS REPORTED IN THIS STUDY

In those parts marked with heavy transverse lines traces of visual tissue were found but probably unfunctional. The cerebral lesions in Group V were less extensive, only dorsal views of the reconstructions being given. For each diagram, the figure at the left is the identification number of the case used in the tables and the text; that at the right, the percent age of the cortex removed.

Subgroup IIIa

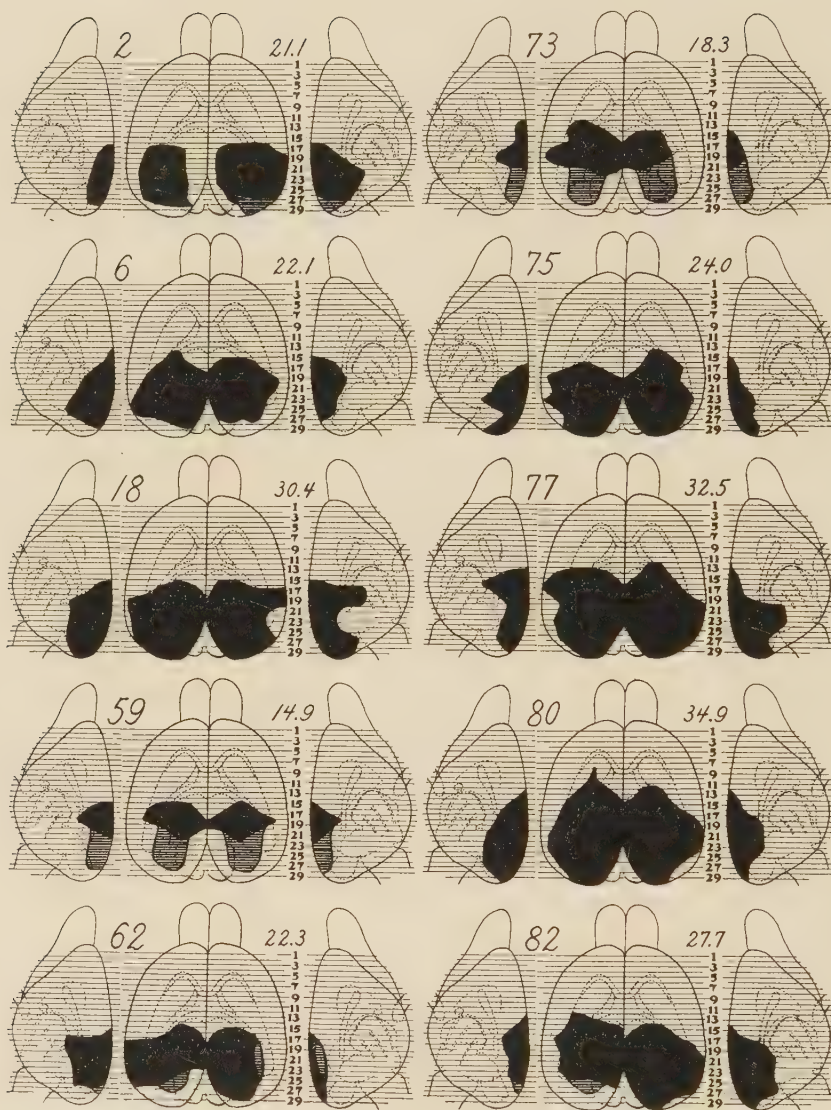


PLATE 1
SUBGROUP IIIa

Subgroup IIIb

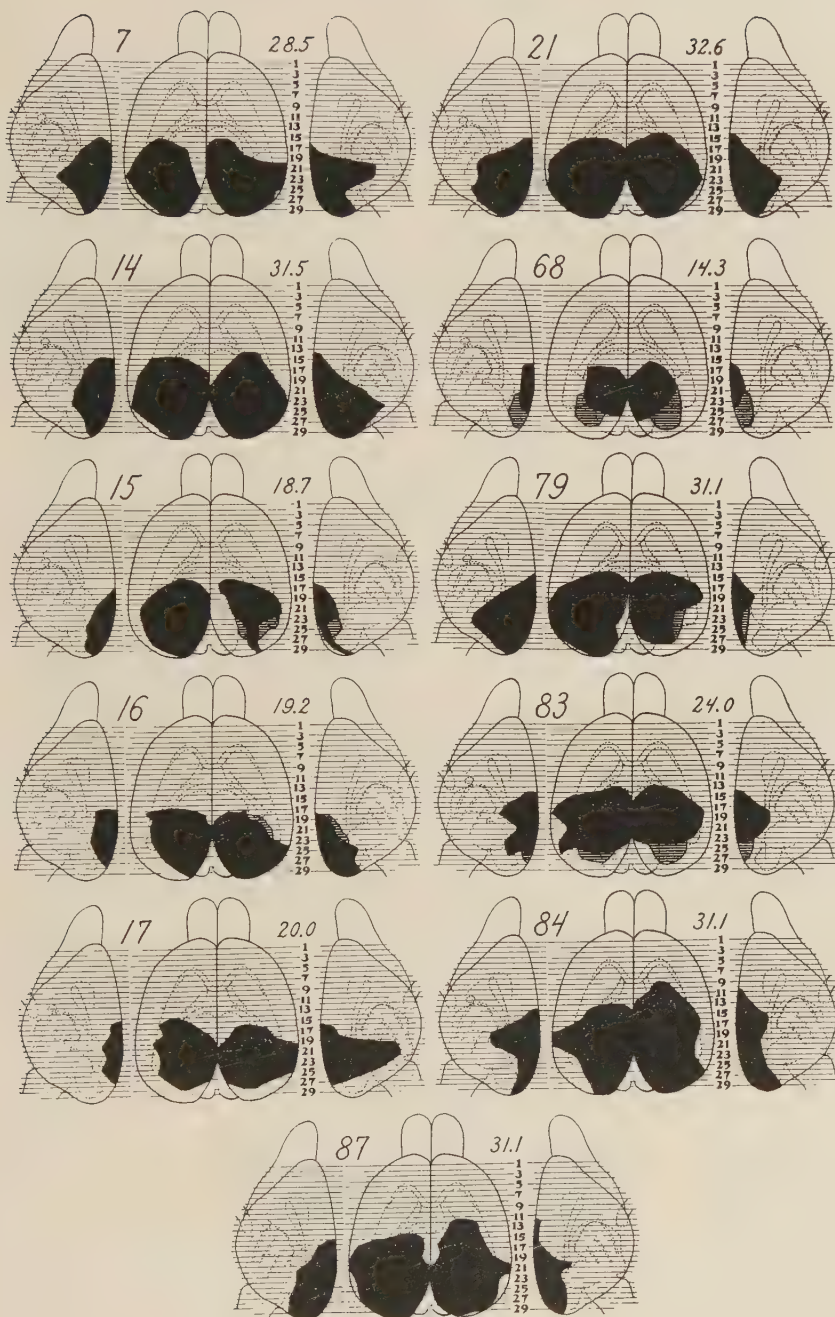


PLATE 2

SUBGROUP IIIb

Subgroup IVa

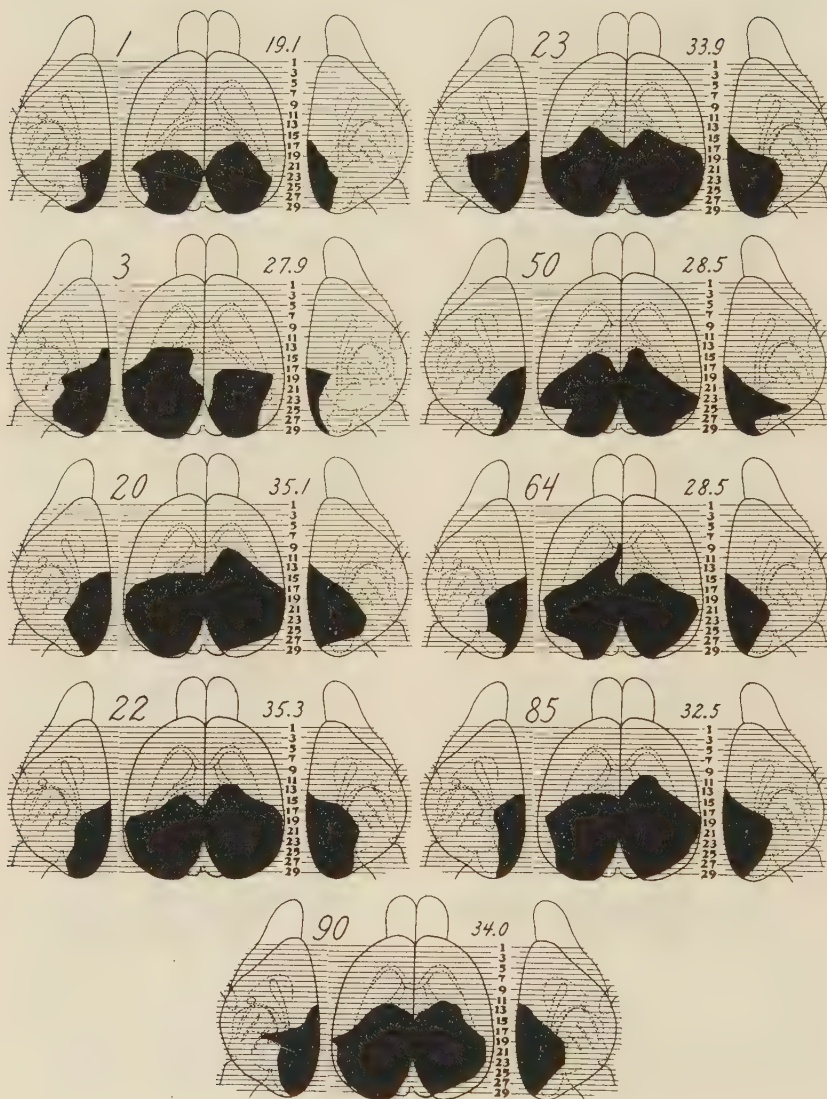


PLATE 3
SUBGROUP IVa

Subgroup IVb

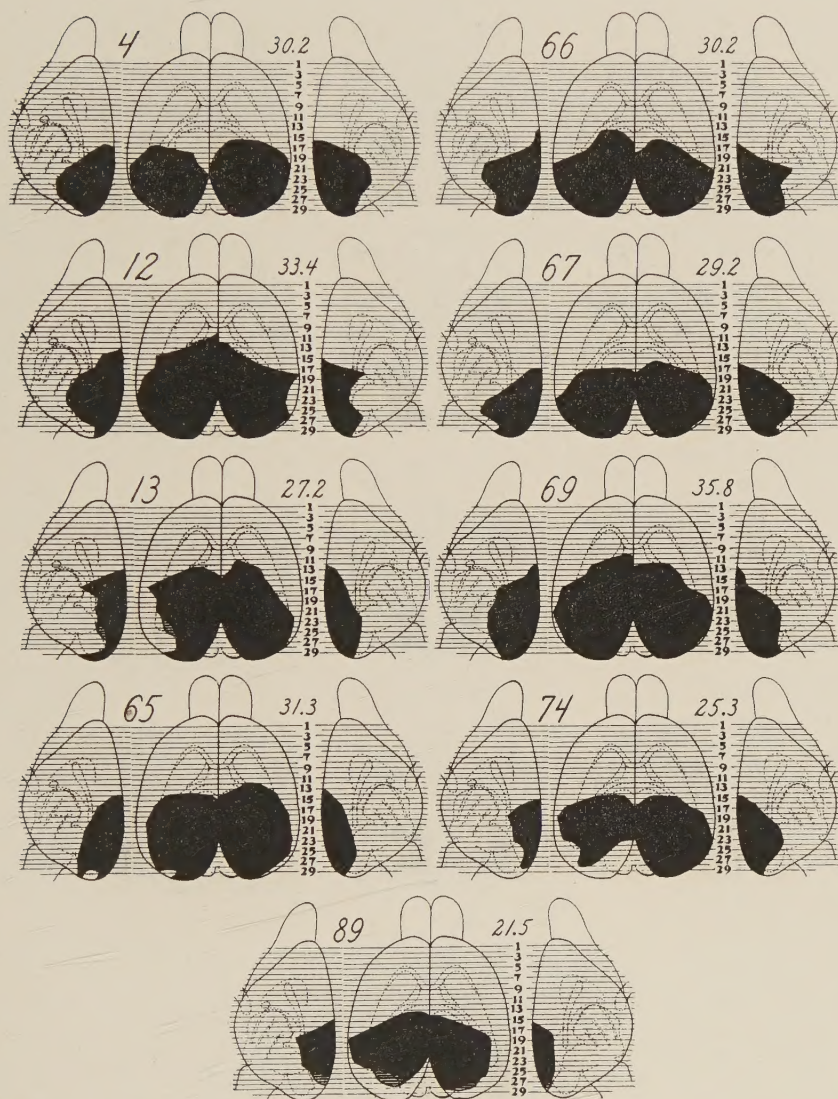


PLATE 4
SUBGROUP IVb

Group V

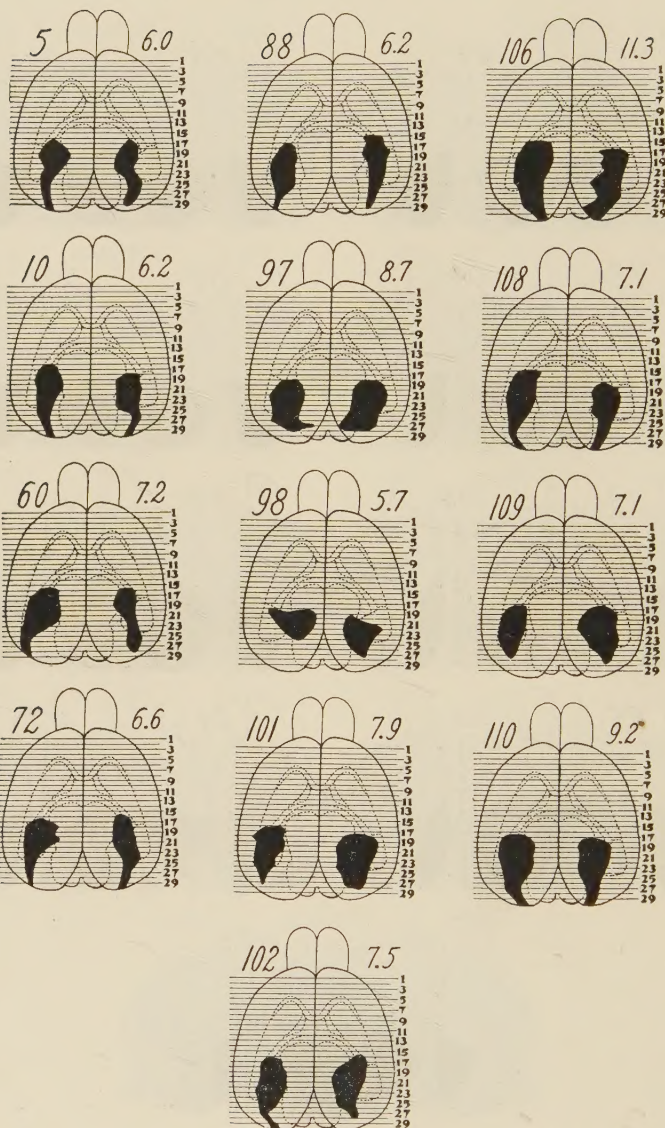


PLATE 5

GROUP V

